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Modifications in the representation and control of finger movement sequences with learning

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A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Neuroscience

Abstract

From typing to playing the piano, sequences of finger movements are essential in our everyday lives. To become skilled at any task, takes practice and determination. To remember and perform a sequence of movements, we form an abstract mental representation of it. To estimate our performance accuracy, we usually rely on sensory feedback from our environment. For instance, when playing piano, we pay close attention to the tone that is played. To improve performance, we adjust our mental representation by integrating this sensory feedback. The goal of this thesis was to elucidate how the mental representation and feedback control of finger movement sequences change with training. We first examined whether the mental representation of a movement sequence can be shaped early in training and how this modulation impacts performance long-term. To this end, we used a discrete sequence production task, in which participants performed sequences of finger presses on a keyboard-like device. We influenced participants' initial representation to be either beneficial or detrimental to performance and estimated how these instructions impacted subsequent performance. Participants' performance was continuously influenced by the instructions throughout a three-week training period. Only if participants abandoned the detrimental instruction could they improve their performance. Next, we investigated how feedback control changes across training. Using the same task, we probed feedback integration over four days by either delaying or advancing the time at which participants received the sensory feedback from the keypress. We found that the feedback perturbations consistently slowed or advanced participants' performance on the perturbed press in accordance with the direction of the perturbation. Nevertheless, the amount of behavioural adjustment decreased with training, suggesting a reduction in feedback integration. In both studies, we could show that the mental representation of skilled movement sequences was hierarchically organized. In summary, this thesis provides novel insights into the change in representation and control of finger movement sequences with training.

Keywords

Motor learning, Finger movements, Sequences, Mental representation, Sensory feedback, Motor control

Summary for Lay Audience

Sequences of movements are essential in our everyday life, from tying shoelaces to playing tennis. By combining simpler movements into longer actions, we can perform movements with sublime artistry such as playing a Beethoven sonata on the piano. To be able to learn and modify such sequences of movements, we need to hold and modify them in our mind. To do so, we represent them as an abstract organization in our brain, which is also termed a mental representation. One key question is how does practice change the mental representation of a movement sequence. One factor that might influence learning is the instructions we receive – through teachers, parents, or other types of media (e.g., YouTube). Such instructions are commonly thought to advance learning. Nevertheless, in some cases, instructions can hinder learning. In the first part of this thesis, we investigated whether providing beneficial or detrimental instructions during the early phase of learning can shape the mental representation and performance of a movement sequence long-term. We found that over a three-week training period, the instructions continuously impacted participants' mental representation and performance. Only if participants were able to abandon the detrimental instructions could they improve their performance. The second part of this thesis investigated how we use sensory feedback during movement execution. For example, when playing the piano, we pay close attention to the produced tone. If we hear a wrong tone, we adjust which key is pressed. This illustrates the importance of sensory feedback during movement sequence execution. While we rely heavily on sensory feedback early in training, it has been suggested that we use it less with practice. To test this, we modified the sensory feedback participants received upon a keypress by delaying or advancing it by a small amount of time. We found that while sensory feedback was indeed less used as learning progressed, the perturbation still significantly influenced participants' performance, by slowing or speeding up their movement execution in accordance with the perturbation direction. Together, this thesis investigated how instructions shape the mental representation of sequences and how feedback is integrated during movement execution.

Co-Authorship Statement

A shortened version of **Chapter 2,** which excludes the results from the algorithm, has been published. The experiment was designed and coded by myself, Atsushi Yokoi and Jörn Diedrichsen. I collected the data, analyzed it, and wrote the manuscript with help from Jörn Diedrichsen, Atsushi Yokoi, and Paul Gribble.

The citation is:

Popp, N. J., Yokoi, A., Gribble, P. L., Diedrichsen, J. 2020. The effect of instruction on motor skill learning processes. Journal of Neurophysiology, 125, 5, 1449-1457.

Chapter 3 is under review at Journal of Neurophysiology. The experiment was designed by myself, Jörn Diedrichsen, and Paul Gribble. Carlos Hernandez Castillo constructed the haptic device and helped me program the task. I collected the data, analyzed it, and wrote the manuscript with helpful comments from Jörn Diedrichsen, Carlos Hernandez Castillo, and Paul Gribble.

Acknowledgments

First and foremost, I want to thank my supervisors Dr. Paul Gribble and Dr. Jörn Diedrichsen for their guidance over the past five years. Through their supervision, I have grown as a scientist and have learned a great deal in terms of computational analyses, writing, and experimental design. I am grateful for their patience and for the opportunities I received.

I would also like to thank the members of the Gribble and Diedrichsen lab (both past and present). Thank you for being wonderful colleagues and friends, for all the coffee chats, lunches, rants, feedback, and help. A special thank you to Eva, who has been a wonderful friend and collaborator over the past years and for valuable feedback on my thesis drafts. Similarly, I want to thank Susan for always having an open ear.

Thanks to the Superlab and the whole Brain and Mind Institute community for cultivating an inclusive and welcoming environment. I want to especially thank my advisory committee: Dr. Jody Culham, Dr. Jessica Grahn, and Dr. Andrew Pruszynski for providing valuable feedback on my projects and for the words of encouragement.

Finally, I would like to thank my mother and my partner Carlos for their encouragement and support. I am especially grateful for the support of my mother, who enables me to pursue any dream that I have. Who supported me in pursuing my academic career, even if it meant that I would live in a different country or even continent. And I want to thank Carlos for his continuous support. He keeps me grounded and tries to make me see things from different perspectives.

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List of Abbreviations

ANOVA	Analysis of variance
BAC	Basic action concept
CI	Confident interval
DSP	Discrete sequence production task
EEG	Electroencephalography
EM	Expectation-maximization
EO	Early onset
fMRI	Functional magnetic resonance imaging
HZ	Hertz
IPI	Inter-press Interval
LCD	Liquid crystal display
LR	Late release
LRA	Linear resonant actuator
M1	Primary motor cortex
MT	Movement time
MS	Milliseconds
N	Newton
O	Onset
P	Peak
PRE-SMA	Pre-supplementary motor area
R	Release
S1	Primary somatosensory cortex
SD	Standard deviation
SDA-M	Structural dimensional analysis of mental representation
SE	Standard error
SMA	Supplementary motor area
SRTT	Serial reaction time task

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Chapter 1

1 General Introduction

1.1 Preamble

Throughout our lifetime we acquire a diverse set of motor skills. It takes practice and repetition to become skilled at any movement, but eventually, it becomes smooth and effortless. Movements are rarely performed in isolation, but rather are strung together into longer actions. For example, when making a cup of coffee, multiple movements are connected, over time becoming bound into a rhythm that is executed similarly every morning. An action that consists of movements that are strung together and performed in a sequential order is also termed a movement sequence. Linking movements reduces the mental effort needed to complete a task, enabling efficient execution of complex actions. In this manner, our tiredness in the morning does not disrupt the actions needed to produce that precious cup of coffee.

Sequencing movements also affords us the execution of sublime artistry, such as a pianist playing a Beethoven sonata or a ballet dancer executing multiple pirouettes on pointe shoes. Such impressive skills demonstrate that our bodies are capable of astonishing feats of movement. Nevertheless, to achieve them with such apparent ease, practice is crucial – be it several iterations for coffee making or years of practice for a professional pianist (Ericsson et al., 1993; Hayes, 2013).

In this thesis, I explore how the mental representation and control of movement sequences develops with training. To investigate these topics, I studied sequences of finger movements. Finger movement sequences are

essential in our daily activities. Take for example the finding that in 2001, 78% of the workforce in Canada used a computer keyboard in their workplace daily (Marshall, 2001). In light of the COVID-19 pandemic, the use of computers and other technologies has also increased (De' et al., 2020; Vargo et al., 2021), amplifying the reliance on finger movements to complete various tasks – from communicating with colleagues to online shopping. Our fingers allow us to perform a variety of dexterous movements such as object manipulation, grasping, or performing sign language. Well-specified anatomical connections (Rathelot and Strick, 2009; Strick et al., 2021) provide us with a clear understanding of the neural processes involved in finger movements. And our ability to individuate our fingers (Hager-Ross and Schieber, 2000) enables a multitude of experimental design manipulations. Therefore, studying finger movement sequences is a powerful experimental paradigm to investigate the representation and control of movement sequences.

I will present two data chapters in the body of this thesis. In the first chapter, we investigated the relationship between the organization of mental representations and performance. To do so, we influenced participants' initial mental representation to be either beneficial or detrimental to performance and examined how this manipulation impacted ultimate performance after three weeks of training. The second chapter investigated how sensory feedback is used to adjust ongoing execution of finger movement sequences. By perturbing participants' feedback, we were able to examine how feedback integration changed across training. Together, these chapters provide novel insights into the control and representation of finger movement sequences.

In the following sections of this introductory chapter, I will first discuss the type of mental representations that have been proposed to underlie the execution of movement sequences. Then, I will examine what factors influence the initial representation of movement sequences and how subsequent training modulates this representation. Thereafter, I will deliberate on the role of feedback during

movement sequence execution. Lastly, I will provide an overview of the subsequent thesis chapters.

1.2 Theories of sequence representation

While sequences of movements have been of interest to neuroscientists for decades, the organization of sequences is still elusive to date. The terms ‘organization’, ‘representation’, and ‘mental representation’ are used interchangeably in this thesis and denote how movement sequences are represented and controlled by the brain. Depending on the theory, this organization can vary from a single layer (Keele, 1968) to a highly structured hierarchical organization with multiple levels (Rosenbaum et al., 1983). Additionally, the type of characteristics that are represented can range from being directly bound to the motor output (e.g. combinations of muscle commands) to more abstract (e.g. sensory consequence or rhythmic features).

1.2.1 Response chaining

One of the first organizations proposed was response chaining (**Figure 1.1A**), where the feedback received from the execution of one movement triggers the initiation of the subsequent movement (James, 1890; Watson, 1920). This type of representation is analogous to a domino effect, where once the first movement is set in motion, this triggers the next movement, which in turn triggers the one after that, and so on until all movements have been executed. This mechanism can explain well-associated movements such as playing a musical piece where the order of movements is pre-determined and not variable (Greenwald, 1970). Nevertheless, two key findings led to the realization that this organization is not applicable to a variety of movement sequences: first, movements can be executed without the need for sensory feedback (Lashley, 1917); and second,

certain types of actions can be reused in different contexts and do not rely on pre-specified associations (Lashley, 1951). This is obvious in speech where different sounds and words are interchangeable and can be freely rearranged (Browman and Goldstein, 1990; Lashley, 1951).

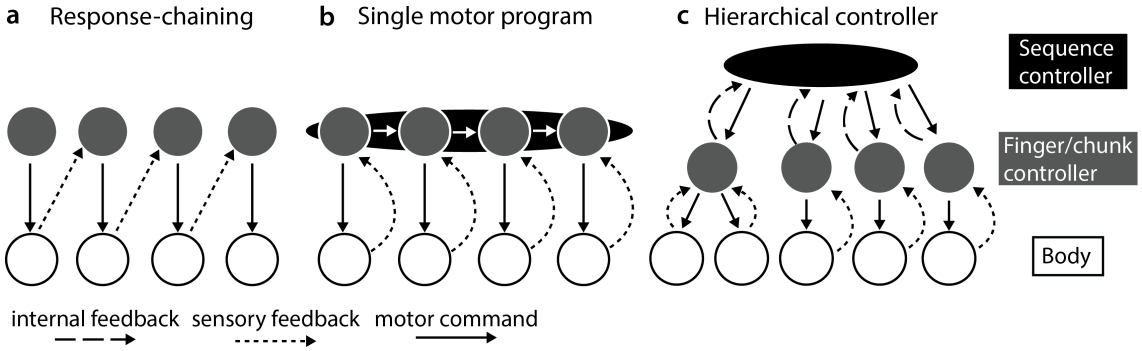


Figure 1.1. Proposed representations underlying movement sequence execution.

(a) In a simple response chaining organization, each motor command is driven by the feedback of the previous movement. **(b)** In the single motor program, the movements are preplanned and executed without the need for sensory feedback from the fingers (i.e. white arrows). **(c)** In a hierarchical organization, each controller is governed and governs one other controller (here similar to tree-transversal structure). Sensory feedback is fed back from the body to the finger controllers (or chunk controllers). Press completion is fed back to the hierarchical controller who sends an initiation signal for the next movement(s) to the finger controller, who then initiates the next movement(s).

1.2.2 Single Motor Program

In response to critiques of response chaining, a new type of “flat” organization was proposed, where movements are still organized serially, but feedback is no longer necessary to trigger subsequent movements (**Figure 1.1B**). This type of organization is also referred to as a single motor program (Keele, 1968). Each motor program stores the muscle commands required for the execution of a single movement sequence. This idea was driven by Lashley's (1917) finding that patients who lost all sensation in their limbs could still produce accurate movements. Therefore, this type of organization introduced the idea of a motor plan, meaning that movements can be preplanned and stored in the brain before execution, which reduces the need for sensory feedback.

The assumption that a flat organization results in a multitude of separate motor programs, where each specifies the exact set muscle commands, implies that such representations cannot be generalized across movement sequences. Therefore, performing a movement sequence similar to an already practiced sequence should be no different than performing a completely novel sequence. This prediction has been refuted on multiple occasions (Panzer and Shea, 2008; Verwey, 2001; Yokoi et al., 2018). Namely, it has been demonstrated that participants can generalize their performance gains to novel sequences that share movement patterns with the previously practiced sequence (Sakai et al., 2003).

On the flipside of generalization, this flat organization also predicts the absence of interference effects. If each sequence is stored as a single motor program, no detrimental effects are expected when learning similar sequences. However, previous learning of a sequence can hinder the learning of a novel sequence when it is only partially modified (Krakauer et al., 2005; Panzer et al., 2006). Therefore, motor programs are too autonomous to account for generalization and interference effects. In light of this, researchers have expanded the motor program idea. Schmidt (1975) for instance suggested a

“generalized motor program”, which is an abstract representation of the movements required for a class of actions (Summers and Anson, 2009). He suggested that the timing and amplitude of motor program commands can be linearly scaled, which allows for a more diverse execution of the same sequence. Thus, a more abstract motor program could account for some of the discussed findings.

Another issue concerns the biological plausibility of a motor program in terms of its neuronal underpinnings. Early propositions focused on the primary motor cortex (M1) as the functional location of motor programs (Wickens et al., 1994). Because of its prominent role in movement execution, it was considered as the prime candidate to encode movement sequences. Previous research has indeed reported findings consistent with this idea (Matsuzaka et al., 2007). For instance, Karni and colleagues (1998, 1995) reported that M1 activity was greater for a trained sequence compared to an untrained sequence, which they interpreted to imply a more extensive representation for the trained sequence in M1. Nevertheless, recent experiments, including work from our lab, have found little to no evidence that M1 encodes sequence identity (Berlot et al., 2020; Beukema et al., 2019; Russo et al., 2020; Yokoi et al., 2018; Zimnik and Churchland, 2021). Rather, these studies demonstrate that M1 activity best represents elemental movements (i.e., single finger movement). In contrast, higher-order areas including supplementary motor area (Hikosaka et al., 2002), premotor, and parietal cortices have been found to encode sequence characteristics (Berlot et al., 2020; Yokoi et al., 2018; Yokoi and Diedrichsen, 2019). These findings suggest a wide network of brain regions associated with the representation of movement sequences (Berlot et al., 2018; Lashley, 1950) rather than a single locus as suggested by a flat representation.

Overall, while a “flat” organization provides a simple, straightforward, and elegant proposal of how movement sequences are represented, it is unable to explain the variety of behavioural and neuronal findings.

1.2.3 Hierarchical representation

In light of the evidence against flat organizations, hierarchical representations of finger movement sequences have become the most viable framework (Book, 1908; Botvinick et al., 2009; Collard and Povel, 1982; Gallistel, 1980; Hikosaka et al., 2002; Pew, 1966; Rosenbaum et al., 1984, 1983; Yokoi and Diedrichsen, 2019).

In this type of organization, sequences are represented across multiple interconnected layers (**Figure 1.1C**), with layers representing movement sequences at different degrees of abstraction. Rosenbaum and colleagues (1983) proposed a specific type of hierarchical organization, called a “tree-transversal structure”. It consists of movement elements (“Body” in **Figure 1.1C**) that give rise to the motor output and control elements (“Finger controller” in **Figure 1.1C**) that are connected to other elements in the hierarchy (Collard and Povel, 1982). Two criteria govern this structure: (a) every control element has to be connected and regulate at least one element of a lower level in the hierarchy (movement or control element). And (b) excluding the element at the top of the hierarchy, each element is supervised by precisely one control element (Rosenbaum et al., 1983). This creates a tree-like structure that branches out from a single point (**Figure 1.1C**). In this framework, the time between the execution of two movements depends on how many nodes have to be traversed along the way. The finding that inter-response intervals vary in duration, depending on the sequence length and position within the sequence (Rosenbaum et al., 1983; Sternberg et al., 1978) supports this structure. This framework can also account for generalization and interference effects as well as for differences in error distribution (Povel and Collard, 1982; Rosenbaum et al., 1983). More broadly, hierarchical organizations have been applied to studies on speech (Sternberg et al., 1988; Uddén et al., 2020), sports (Schack, 2004), and across different areas of musical processing (Fitch, 2013; Lerdahl et al., 1985; Rohrmeier, 2011).

To summarize, evidence supports a hierarchical organization of movement sequences. Nevertheless, it is less well understood how these hierarchical representations develop and change with extensive training and whether their specific organization relates to performance. I will discuss some of the findings related to these questions in the next section.

1.3 The acquisition and modification of a sequence representation with practice

So far, I have discussed what type of mental representation could underlie the control of movement sequences, but a remaining question is how these representations are learned in the first place. When first learning a novel movement sequence, for instance, a musical piece on the piano, we use a single item selection process whereby we treat each part of the sequence as a separate action (Diedrichsen and Kornysheva, 2015). Performance in this early stage is marked by slow execution with long breaks between movements (Rand et al., 2000; Rhodes et al., 2004). As we become more familiar with the execution of the musical piece, we start to combine movements into so-called “chunks” (Gobet et al., 2001; Lashley, 1951; Verwey, 1996; Verwey et al., 2010; Verwey and Eikelboom, 2003).

The formation of chunks is behaviourally characterized by changes in the timing between movements. The inter-response interval between movements is more rapid if the movements are within a chunk than if they are at a chunk boundary (Verwey and Dronkert, 1996). This is clearly visible in phone numbers, where the visual structure (e.g., 226-521-4870) is also evident during vocalization or typing. The emergence of chunks early in training (Verwey and Dronkert, 1996) is suggested to be driven by working memory constraints (Bo and Seidler, 2009; Seidler et al., 2012; Solopchuk et al., 2016). Because movement sequences are often longer than the “magical number 7” (Miller, 1956), chunks

are assumed to aid memorization by breaking longer sequences into smaller parts (Chekaf et al., 2016). Research further points to the ability of holding four chunks in short-term memory (Cowan, 2001).

The emergence of chunks has also been recognized as a behavioural identifier of a hierarchical organization (Afraimovich et al., 2014; Fonollosa et al., 2015). While at first each movement element is governed by a separate controller, through chunking movements become linked and governed by the same controller (**Figure 1.1C**). Together these distinct chunk controllers make up one layer of the hierarchical organization. Investigating the chunking process by inspecting the temporal execution pattern of sequences provides a valuable proxy of early movement sequence representation.

1.3.1 Measuring mental representation of movement sequences

A recent approach utilizes these movement chunks to measure the hierarchical representation of movement sequences. The “structural dimensional analysis of mental representation” (SDA-M) was proposed by Schack (2012) and is based on the idea of basic action concepts (BACs). These can be understood as functional parts of a sequence and strongly relate to the idea of movement chunks. The first necessary step in this method is to determine the BACs for a given movement sequence based on opinions from experts, experimental observations, biomechanical features, and participants’ perceptions. For instance, these BACs were determined in the pre-activation phase of a tennis serve: ”(1) ball throw, (2) forward movement of pelvis, (3) bending the knees, and (4) bending the elbow” (Schack & Mechsner, 2006; p. 78). Once the BACs have been determined, the next step involves a split procedure to create a distance scaling between the different BACs. In this procedure, reaction times are measured while the participants are asked about the perceived similarity between the BACs. A hierarchical cluster analysis then translates the obtained

BAC similarity and reaction time measures into a hierarchical organization, with dimensionality reduction applied to uncover the different clusters. Lastly, it is assessed whether the resulting organization is invariant across participants and within the individual (Schack, 2012).

Schack and colleagues have applied this technique to a multitude of movement sequences across a variety of sport disciplines. They demonstrated that highly trained individuals showed hierarchical representations that coincided with the biomechanical and functional properties of the movement sequence and were fairly invariant across participants (Bläsing et al., 2009; Schack, 2003; Schack and Mechsner, 2006; Velentzas et al., 2010). In contrast, novices showed representations that were more variable across participants and less hierarchically organized. Overall, these results suggest a potential link between the structure of the mental representation and the performance of a movement sequence.

While this technique has provided an elegant way to measure the representation of movement sequences, it does, however, rely on the participants' perception of the relationship between the movement elements rather than estimating mental representation directly from their motor output. Therefore, it remains unclear whether motor performance is causally related to the mental representation and how this relationship is modified with training. By solely correlating the performance of participants with changes in mental representation, these studies were unable to provide a causal link between the two variables. Hence, an important missing piece to understanding this relationship is to manipulate the initial representation and examine how it impacts performance.

1.3.2 Factors influencing the early representation of movement sequences

In order to manipulate the initial mental representation, it is crucial to recognize the factors that can influence the formation of participants' movement chunks at the beginning of training. In the study of finger movements sequences, several factors have been found to modulate early inter-response interval patterns. One such factor is the structure of finger movements within the sequences, which includes characteristics such as regularities, repetitions, or reversals (de Kleine et al., 2009; Koch and Hoffmann, 2000; Verwey and Eikelboom, 2003). Another factor is the visual presentation of the sequences, as previously shown by the phone number example. A last factor I want to address is the timing of execution. To study this effect on participants' chunk structure, Summers (1975) presented cues indicating which finger had to be pressed at varying time intervals during a finger sequencing task. Some cues were presented quicker in succession (100 ms), while others had a longer pause between presentations (500 ms). Participants were instructed to execute the sequences in this pre-specified rhythm even for trials where they had to perform the sequences from memory. After an initial set of training blocks, Summers (1975) switched the goal of the task and asked participants to perform the sequence as quickly as possible from memory. He found that despite the removal of timing constraints, participants still paused longer at the locations that were originally separated by longer inter-response intervals. This suggested that temporal patterns imposed early in training impacted participants' chunk structure even once the temporal constraints were removed (Verwey et al., 2009; Verwey and Dronkert, 1996). Altogether, these studies provide evidence that it is possible to shape participants' initial mental representation by imposing certain sequence and experimental characteristics.

1.3.3 Changes in chunking with training

Once an initial representation has formed, how is it modified with training? Practice is accompanied by a multitude of behavioural modifications. The most readily identifiable is the decrease in time needed to execute the movement sequence; making it a hallmark of motor sequence learning (Abrahamse et al., 2013; Berlot et al., 2020; Korman et al., 2003). This increase in speed has been related to several distinct processes including increased accuracy (Woodworth, 1899), faster movement selection (Ariani and Diedrichsen, 2019; Haith et al., 2016; Hardwick et al., 2017), and more rapid movement planning (Ariani and Diedrichsen, 2019; Wong et al., 2014). Behavioural changes are believed to rely on improvements related to the mental representation. At present, however, we still do not have a clear understanding of how these behavioural changes are associated with modulations in sequence representation.

One possible way to measure changes in sequence representation more directly with training is to assess changes in participants' chunk pattern. A large body of studies has demonstrated that the number of chunk boundaries decreases with practice (e.g. the longer inter-response intervals), which results in longer chunks (Acuna et al., 2014; Solopchuk et al., 2016; Song and Cohen, 2014; Verstynen et al., 2012; Wymbs et al., 2012). The location of these boundaries also shifts with practice (Acuna et al., 2014; Fonollosa et al., 2015; Wymbs et al., 2012). Therefore, if we assume that these adjustments in chunk structure directly relate to a modulation of sequence representation (Fonollosa et al., 2015), then these findings provide supporting evidence of training-induced modulations. By reducing the number of chunk boundaries, we increase execution efficiency as we reduce the amount of longer inter-response intervals between movements (Ramkumar et al., 2016). This could imply that in order to achieve the maximum efficiency, the ultimate goal of sequence execution should be to execute the sequence as a single chunk (Servan-Schreiber and Anderson, 1990). This could further signify a change in representation from hierarchical to flat with extensive training. In opposition to this idea, using the previously

discussed SDA-M technique, Frank and colleagues (2013, 2016) found that training resulted in an increase in functionally relevant clusters which represents greater hierarchical organization. Therefore, it is still unclear whether extensive training strengthens or weakens the hierarchical representation of sequences.

One difficulty that can distort the results from chunking experiments is that changes in execution speed can bias the measurement of chunk boundaries. Due to the increase in speed, we may simply no longer be sensitive to changes in inter-response intervals and mistakenly label a faster sequence as not containing chunks. Therefore, we need a more systematic and sensitive examination of how the chunk structure changes over (a prolonged period of) time. Recent modeling efforts have proven valuable in untangling measures of chunk boundaries and changes in overall execution speed (Acuna et al., 2014).

In summary, to get better understanding of the relationship between mental representation and performance it is important to a) manipulate the mental representation and examine how this impacts performance over time, and to b) carefully examine modulations in mental representation over time by considering changes in behaviour, such as improvements in speed.

1.4 The role of feedback in movement sequence control

So far, I have discussed the type of organizations that could underlie the representation of movement sequences and how these representations are shaped by external variables and training. Another important factor that shapes sequence performance and might influence sequence representation is sensory feedback. During movement execution, we receive sensory input from various modalities. This input provides us with feedback regarding the accuracy and timing of our movements. For example, when playing the piano, the sensation felt on the fingertips when pressing the key, the visual feedback of the depressing

key, and the tone that is heard, all provide us with valuable information that can be used to estimate and adjust performance.

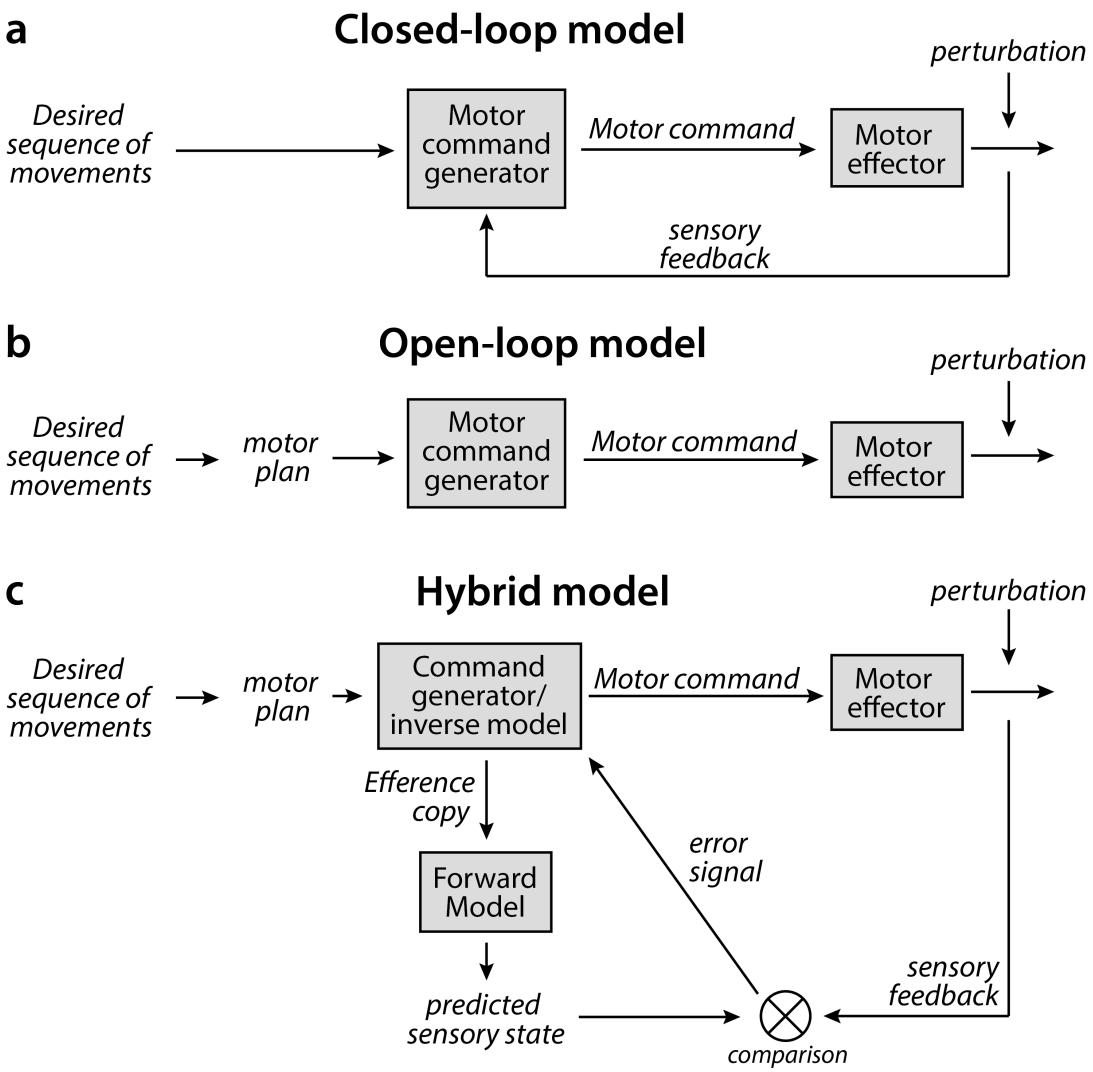
Sensory feedback is used to correct movement errors in two ways: a) through an online process by which it is used to adjust ongoing movements directly after the error occurred and b), through and an offline process where it is used to adapt the motor commands between executions (Seidler et al., 2013). Here, I will focus on the feedback processes involved in the online corrections during execution. Whereas the integration of sensory feedback to adjust ongoing movements has been extensively studied in reaching movements and adaptation studies (for reviews see Cluff et al., 2015; Scott, 2012; Shadmehr et al., 2010), less is known about the importance of feedback in sequences of movements and especially in the execution of finger movement sequences. It is also unclear how feedback is integrated in the potentially hierarchical representation of finger movement sequences. To provide an overview of the current literature on this topic, I will first discuss prominent views regarding the general integration of feedback in motor control and how this integration changes with training. Afterwards, I will address findings from synchronization studies, which are currently the prominent model for examining feedback control in finger movement sequences.

1.4.1 Open and closed-loop control

Researchers have long acknowledged the important role of sensory feedback in motor control. One particular theory in which feedback is particularly important to motor control is the closed-loop theory (**Figure 1.2A**). Spear-headed by Adams in 1971, it proposes that feedback is continuously used to adjust and inform the execution of a motor skill. In this view, sensory feedback is essential to the execution of movement sequences throughout skill acquisition, even once actions have become automatized (Proteau, 1992). On the other end of the

spectrum stands the concept of open-loop control (**Figure 1.2B**). It proposes that an action can be executed and planned without the need for sensory feedback (Lashley, 1917). A strong argument for open-loop control stems from the idea that very fast movements are too fast for feedback to play a role (Gerdes and Happee, 1994; Hollerbach and Flash, 1982; Schmidt and McCabe, 1976). The finding that patients and monkeys who lost peripheral input (i.e., deafferentation) are still capable of movement (Polit and Bizzi, 1979; Rothwell et al., 1982; Taub et al., 1975), further strengthens this theory. While these two theories are extremes of the spectrum, movements are likely driven by both types of control, with some movements relying more on open-loop control while others rely more on feedback control.

Figure 1.2 Feedback control models.
(a) In a closed-loop model sensory feedback is continuously used to update movement execution. **(b)** Feedback is not used to adjust movement execution in an open loop model. A motor plan enables movement execution without the need for feedback. **(c)** Depicts a “Hybrid model” which uses internal models to adjust and predict movement output during execution. An inverse model specifies the motor commands and the forward model uses an efference copy of these commands to specify the predicted sensory state at any given moment. Sensory feedback identifying the actual state of the movement is then compared to the predicted state and any discrepancies result in corrective commands that are integrated during movement execution.


a
Closed-loop model
perturbation
Desired sequence of movements
Motor command generator
Motor command
Motor effector
sensory feedback
b
Open-loop model
perturbation
Desired sequence of movements
motor plan
Motor command generator
Motor command
Motor effector
c
Hybrid model
perturbation
Desired sequence of movements
motor plan
Command generator/ inverse model
Motor command
Motor effector
Efference copy
error signal
Forward Model
sensory feedback
predicted sensory state
comparison

1.4.2 Internal models

Internal models were originally proposed to overcome the sluggishness of feedback control (Kawato, 1999; Wolpert and Kawato, 1998), but have since reached wide acceptance in the motor control field, as they can provide an opportunity for the integration of feedback and open-loop control. Internal models estimate movement execution and the consequences of our movements in two ways (Wolpert et al., 2001; Wolpert and Kawato, 1998). The *inverse model* computes the motor commands that are needed to reach a desired movement state. The *forward model* predicts the sensory outcomes anticipated from the motor commands of the inverse model (**Figure 1.2c**). For example, when playing music, one can anticipate the specific tones and rhythm that should be heard upon execution.

Many theories assume that our mental representation codes the sensation associated with movement execution (Bernshtein, 1967; Fowler and Turvey, 1978; Prinz, 1987). This assumption has also been experimentally supported (Elsner and Hommel, 2001; Greenwald, 1970; Schack and Mechsner, 2006). For instance, Mechsner and colleagues (2001) demonstrated that the tendency for mirror symmetry during bimanual movements stems from the perceptual information and not from muscle coactivation. They tested how different hand postures affected accuracy when performing synchronous index finger movements with both hands. If the mirror symmetry arises due to synergies of the homologous muscles, then hand posture should matter, as this changes which muscles are activated. They found, however, that participants were most accurate when the perceptual information was mirrored irrespective of whether the same muscles were activated across hands. Furthermore, the worst accuracy was found in a condition where homologous muscles were used. They concluded that perceptual rather than muscle-related mechanisms drive bimanual symmetry.

The predictive power of a forward model reduces the need for sensory feedback (Higgins and Angel, 1970; Jaeger et al., 1979). To overcome the sluggishness of sensory feedback, the forward model utilizes an efference copy of the motor output, which it then compares to its prediction of the desired state. Any discrepancy between the two can be used to induce online corrections without the need for sensory feedback. In predictive environments, such as during self-generated movements (i.e., not due to external disturbances), we rely on an internal model to smoothly adjust our behaviour. For example, when we move our arm while gripping an object, the changes in grip force happen in parallel with the increases in load with no noticeable delay (Flanagan and Wing, 1997; Gallistel, 1980). Thus, instead of sensory feedback, an internal model was used to adjust the grip force. Furthermore, the existence of internal models enables us to ignore sensory feedback that is potentially misleading (Flanagan et al., 2001).

While internal models can overcome the inherent feedback delays through state predictions, there are times when these predictions are inaccurate. For instance, early in training when errors are large and the internal model is still inaccurate, we need to rely on feedback control to adjust ongoing movements (Wolpert and Flanagan, 2001). As internal models are updated with training (Jordan and Rumelhart, 1992), they become more accurate and in turn facilitate movement execution (Hertz et al., 1991; Krakauer et al., 1999; Weir et al., 1989; Wolpert et al., 1995).

To add more flexibility in terms of feedback vs. feed-forward control "Hybrid models" have been proposed (**Figure 1.2C**) that integrate both control types during movement execution (Desmurget and Grafton, 2000; Hoff and Arbib, 1993; Pélisson et al., 1986; Wolpert et al., 1995). In these models, sensory feedback is compared to feed-forward predictions to adjust ongoing movements. One such application is predictive coding which uses Kalman-filtering and updates the state estimation using sensory feedback (Huang and Rao, 2011;

Miall and Wolpert, 1996; Wolpert et al., 1995). In this way the motor system can optimally combine the predicted state and the perceived sensory feedback into a state estimate that guides behavioural modifications. While these models have been successfully applied to explain rapid behavioural adjustments to feedback perturbations in reaching movements (Miall and Wolpert, 1996; Shadmehr and Mussa-Ivaldi, 1994; Wolpert et al., 1995), object manipulation (Flanagan and Wing, 1997) and speech production (Jones and Munhall, 2000), they have, to our knowledge, not been utilized to elucidate feedback integration in finger sequence tasks.

1.4.3 Changes in feedback integration during movement execution with training

It has been proposed that the amount of reliance on feedback versus feed-forward control shifts with practice (Pew, 1966; Seidler-Dobrin and Stelmach, 1998). Specifically, the notion is that in the initial phases of motor skill acquisition feedback control dominates execution, whereas later in training we rely more on feed-forward control. This shift is related to an increase in internal model accuracy with training, which reduces the need to integrate the sluggish sensory feedback (Pew, 1966; Pratt et al., 1994; Schmidt, 1975; Schmidt and McCabe, 1976; Seidler-Dobrin and Stelmach, 1998). This shift has also been reported in electromyography (EMG) activity during movement adaptation (Coltman and Gribble, 2020; Thoroughman and Shadmehr, 1999).

Another line of findings that could further our understanding on the shift in feedback control comes from observations of differences in feedback integration between novices and experts. Yet, findings thus far have been divided in this regard. Some studies using finger sequence tasks reported that novices were impacted to a greater extent by feedback perturbations than experts (van der Steen et al., 2014), while other studies have found the opposite effect (Pfordresher, 2008, 2005). In an experiment involving singing, it was found that

experienced singers responded less to a fundamental frequency shift compared to novices, but showed enhanced aftereffects (Jones and Keough, 2008). The researchers interpreted this finding as the experienced singers depending to a greater extent on internal models compared to novices. While previous research suggests a shift from feedback to feed-forward control with training, several shortcomings need to be addressed to provide a better understanding of this topic. Either studies failed to directly assess feedback integration during movement sequence execution by relying on observations rather than using manipulation, or they did not examine the changes in the same participant sample over a prolonged period of time. One way to address these shortcomings is to probe feedback integration during movement sequence execution by using feedback perturbations and measuring changes in behaviour over an extended training period.

1.4.4 Feedback integration in synchronization tasks

The use of sensory feedback in sequence production has not been well studied. One exception are synchronization tasks. In these studies, participants have to synchronize their finger movements either to a metronome or to a musical piece (Drewing, 2013; van der Steen et al., 2014; Wing, 1977). Two types of synchronization tasks have been primarily used. In the “pseudo-synchronization task” (Flach, 2005; Pfordresher and Palmer, 2002), participants are asked to synchronize their movements with a metronome, which is taken away after a while and participants have to keep executing the movements at the same pace (i.e., same response timing). In the other type of synchronization tasks, participants are asked to continuously synchronize their movements to an external variable such as a musical piece or a metronome (Gates et al., 1974; Kulpa and Pfordresher, 2013; Repp, 2000; van der Steen et al., 2014). To assess feedback integration in these tasks, researchers delay the time at which participants receive the sensory feedback associated with a finger movement.

Some studies have reported that a time delay in sensory feedback presentation leads to an increase in performance speed (Flach, 2005; Pfordresher and Palmer, 2002; Repp, 2000). This speed-up arises to counteract the delay and to preserve the execution rhythm (Flach, 2005; Furuya and Soechting, 2010; Pfordresher and Palmer, 2002). This would suggest a behavioural adjustment that opposes the direction of the perturbation. Other studies, however, have reported a slowing rather than a sped up in performance after a feedback delay (Gates et al., 1974; Kulpa and Pfordresher, 2013; van der Steen et al., 2014; Wing, 1977), which suggests a behavioural adjustment in the same direction as the perturbation. Thus, it is unclear whether feedback perturbations lead to behavioural changes in the same direction as the perturbation or to opposing adjustments. Further, there are two other shortcomings of the previous studies that I want to highlight and that will be addressed in this thesis.

First, the majority of studies investigating sensory feedback perturbations in sequence execution have used synchronization tasks. Research on how feedback perturbations are integrated in non-constrained sequence execution is scarce. Amongst the few studies that have been reported, it has been demonstrated that presenting a lag in visual, haptic, or auditory feedback results in disrupted and delayed performance (Jay and Hubbold, 2005; Long, 1975). However, further research into non-constrained sequence execution is greatly needed.

Second, one critical limitation of the majority of these studies is that they only delayed participants' feedback, but did not assess what happens if the feedback is advanced. Both types of feedback violate expectations, however it is unclear whether both will produce similar or opposing effects on behaviour. Amongst the studies that advanced participants' feedback during a synchronization task, discrepant results were found. One study demonstrated a slowdown in subsequent performance (Repp, 2000), whereas another study reported a speed up (Wing, 1977). To get a better understanding on the

integration of feedback during movement sequence execution, it is important to include time delays as well as advancements when using feedback perturbations.

1.4.5 Wing-Kristofferson model

Lastly in this section, I want to examine a prominent model that has been proposed for the control of movement sequences. The Wing-Kristofferson model (Wing and Kristofferson, 1973) focuses on explaining the control of movement sequences as they are synchronized to an external variable. In this open-loop model, the execution of self-paced movements (such as in the end of pseudo-synchronization tasks) is governed by two processes: a) a central time-keeper that sends a movement initiation signal after a fixed time interval, and b) a motor controller that in turn performs the signalled movement after a certain delay. These two processes are believed to work in parallel to govern the timing of execution. This model has been found to account for a number of behavioural findings. For instance, it predicts the observation that the neighboring inter-response intervals in synchronization tasks are negatively correlated (Ivry et al., 1988; Wing and Kristofferson, 1973). The model accounts for this finding by assuming that the variability of the motor delay and the internally generated intervals are uncorrelated. If the response of the motor controller is delayed on a given movement, this increases the current inter-response interval, as it delays the current onset of the movement. At the same time, it also reduces the next inter-response interval since the timekeeper still sends the next signal after a given time interval irrespective of the motor controller delay. Thus, when measuring the next inter-response interval, it will be shorter than the one before, leading to a negative correlation across neighboring intervals. In a later adjustment of this model, a linear phase corrector was added that can partly correct the timekeeper interval based on the asynchrony experienced on a previous movement (Vorberg and Wing, 1996). This was added to account for

the finding that a feedback perturbation can impact the timing of the subsequent press (Wing, 1977). More recently, Drewing (2013) proposed that the timing processes described in the model account for the sensory consequences of the movements rather than for the movement commands themselves.

While the Wing & Kristofferson model accounts for a number of findings in the synchronization literature, it is unclear whether this model can account for behaviour in situations where synchronization is not required. Without the need to synchronize, the goal of the task shifts. In such non-constrained execution tasks, the main goal is predominantly to perform sequences of movements as quickly and accurately as possible, which is contrary to the requirement of synchronization tasks to preserve a rhythm. Hence, other control mechanisms might be in place to control unconstrained sequences of movements. Overall, understanding how sensory feedback is integrated in fast and non-restrained execution of finger movement sequences remains a research gap that deserves further attention.

1.5 Chapter overview

The overarching goal of this thesis was to further our understanding of the representation and control of finger movement sequences. Specifically, we were interested in understanding how the mental representation of finger movement sequences can be shaped by instructions early in training and how this can impact the ultimate performance after training. This will provide us with further information regarding the relationship between mental representation and performance. Further, we were interested in examining whether sensory feedback is continuously used to adjust movement execution, even after sequences have become skilled. By perturbing the feedback participants received, we were able to probe the idea that feedback integration shifts from feedback to feed-forward control with practice. To achieve these objectives, we

used a discrete sequence production task in which participants performed sequences of movements with their right hand as rapidly and accurately as possible on an isometric keyboard. We provided participants with different types of sensory feedback during execution and measured their force and response timing.

Chapter 2 presents experiments aimed to manipulate participants' initial mental representation where we investigated how sequence representations changed over three weeks of training. To do so, we influenced participants' temporal execution pattern (chunking) early in practice. Participants first practiced smaller parts of the sequence (i.e., chunks), while only later being presented with the entire sequence. By instructing participants' early chunk structure, we were able to directly assess how this initial representation impacted subsequent learning over three weeks. Additionally, we influenced their initial representation to be either beneficial or detrimental to overall performance by considering the behavioural constraints of our keyboard. This enabled us to estimate whether these two types of instructions shaped participants' behaviour to a similar extent. We used an advanced modeling technique to estimate participants' chunking structure over time, accounting for overall changes in speed. In summary, this experiment allowed us to examine how initial instructions can shape participants' early mental representation and whether this representation remains stable across a longitudinal training regimen.

Chapter 3 addresses the question of how feedback is used to adjust the execution of skilled finger movement sequences. To probe feedback integration, we chose to advance or delay the sensory feedback participants received on a single finger press within a sequence. We measured how this small transient feedback perturbation affected behaviour on the perturbed press itself as well as on the subsequent finger presses in the sequence. We trained participants over four days to assess whether the effects of the perturbation changed with practice. Additionally, we performed a second experiment where we examined which

sensory modality (auditory, haptic and visual) impacted participants' performance the most. Furthermore, we were able to estimate what type of representation underlies participants' movement execution and uncover the distinct feedback processes involved in this organization.

In summary, this thesis provides novel insights into the representation and control of finger movement sequences. By manipulating participants' behaviour in a precise and systematic manner, I was able to address shortcomings of previous research and demonstrate the malleability and hierarchical nature of mental representations of skilled finger movement sequences.

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Chapter 2

2 The effect of instruction on motor skill learning

2.1 Introduction

Many motor skills are learned with the help of instructions, be it from peers, parents, teachers, or from videos. Such instructions often break down longer, complicated sequences of actions, for example tying one's shoelaces, into smaller elements that can be more easily remembered and practiced. Thus, instruction help to build up an initial mental representation of the motor skill, which in turn guides physical practice (Green and Flowers, 1991; Hodges and Franks, 2002; Masters, 1992; Meier et al., 2020; Wulf et al., 1998). However, it is unclear for how long these initial mental representations influence motor behaviour. At what point does the learner find an optimal way of performing the action independent of the initial instruction? Furthermore, are some ways of building an initial mental representation of a motor sequence better than others?

We investigated these questions in the context of a discrete sequence production task (DSP), in which participants perform a series of single finger presses as fast as possible while having full knowledge of the sequence (Abrahamse et al., 2013; Verwey, 2001). Learning in this task depends on both cognitive and motor processes (Diedrichsen and Kornysheva, 2015; Wong et al., 2015). Initial performance relies strongly on forming a declarative memory of the sequence (de Kleine et al., 2009; Verwey et al., 2010, 2009; Verwey and Dronkert, 1996). This initial declarative memory (or mental representation) of the motor sequence is often characterized by chunking – the process of breaking down long sequence of items into smaller subsets, which has been shown to aid memorization (Halford et al., 1998; Miller, 1956; Solopchuk et al., 2016). In the

context of movement sequences, this chunked memory representation has been shown to influence the actual motor performance, with participants inserting larger pauses between chunks than between finger presses within a chunk (Verwey, 1996; Verwey and Dronkert, 1996). This cognitively-induced chunking pattern (de Kleine et al., 2009; Verwey et al., 2010, 2009; Verwey and Dronkert, 1996) has been found to remain stable over the course of a few days of practice (Verwey and Eikelboom, 2003).

We hypothesized that the way the initial declarative memory of a motor sequence is chunked will either facilitate or impede subsequent skill learning. To test this idea, we instructed participants to memorize long sequences of finger presses by first practicing smaller 2-3 digit “chunks” on an isometric keyboard-like device. Participants were then trained on the seven 11-digit sequences that were made up of the 2-3-digit chunks that they had learned prior. Each sequence was subdivided and instructed in two different ways: In a counterbalanced within-subject design, half of the sequences for each participant were instructed using an aligned chunking structure, in which the boundaries between chunks were aligned with finger transitions that were difficult to execute. These transitions constituted natural breaking points, and we hypothesized that the participants should be able to use the time needed to execute these transitions to recall the next chunk. Additionally, we kept easy finger transitions, such as runs (e.g. 123), together within a chunk, enabling participants to execute these quickly. The other half of the sequences were instructed using a misaligned chunking structure, in which these easy finger transitions were artificially broken up by chunk boundaries, and difficult transitions were kept within a chunk. We hypothesize that sequences that were learned under a misaligned structure would be executed more slowly. After the instruction phase, participants practiced the sequences over the course of three weeks, allowing us to investigate the influence of the initial instruction on subsequent motor skill learning.

Specifically, we investigated three questions: First, do the initial chunk instructions lead to stable movement patterns that persists over three weeks of training? Second, can different chunk instructions on the exact same sequence lead to movement patterns that are superior or inferior in terms of performance? We hypothesized that sequences learned using the misaligned instruction would be performed slower compared to sequences learned with the aligned instruction. Finally, if we can induce deficits in performance using suboptimal chunk instructions, how long are these maladaptive patterns maintained?

2.2 Methods

2.2.1 Participants

In total forty participants who reported no neurological conditions were recruited for the study (30 females; ages: 19 to 33). Thirty-two of them were randomly assigned to learn the sequences with one of the two chunk sets. Eight additional participants were recruited as a control group that did not receive any chunk instructions. All participants were right-handed based on the Edinburgh Handedness Inventory and completed informed consent. On average, participants had received 4.68 ($\pm$ 5.55) years of musical training, with 55% reported having more than six months of experience playing the piano. While participants with piano experience performed the sequences faster than participants with no experience and the number of practice years correlated with execution speed (MT), the amount of participants' prior musical experience did not have a qualitative influence on participants' chunking behaviour. The study protocol was approved by the ethics board of the University of Western Ontario.

2.2.2 Apparatus

A custom-built five-finger keyboard was used (**Figure 2.1a**). The keys were not depressible but were equipped with a force transducer (FSG-15N1A, Sensing and Control, Honeywell) underneath each key which measured participants' isometric force production with a repeatability of <0.02 N and a dynamic range of 16 N (Wiestler et al., 2014; Wiestler and Diedrichsen, 2013; Yokoi et al., 2017). The measured force at each key was digitally sampled at 200 Hz.

2.2.3 Discrete sequence production task

We used a discrete sequence production task (DSP) in which participants executed sequences of two, three, or 11 keypresses as fast as possible while keeping their error rate under 15%. Each finger was associated with a number (thumb = 1, index = 2, middle = 3, ring = 4 and little = 5; **Figure 2.1a**). Each trial started with the visual presentation of the sequence to be executed and was completed once the participants pressed the amount of presented numbers.

A keypress was registered when the measured force first exceeded 1.5 N. A key release was marked when the force measured at the same key first fell below 1 N. The magnitude of the force applied to each key was represented by five lines on an LCD monitor, with the height of the line representing the force at the corresponding key. No pause between presses was required and thus some co-articulation between fingers emerged with faster execution. However, to prevent participants from pressing more than several keys at once, the previously pressed key had to be released before a new key could be registered as pressed.

Immediately after the keypress threshold was reached, participants received visual and auditory feedback. If the correct key was pressed, the color of the corresponding digit changed from white to green and a sound was

presented (same sound for each key). If the incorrect key was pressed, the cue turned red and a lower-pitch sound was presented.

After each trial participants received points based on their accuracy (whether all presses in the sequence were correct) and movement time (MT; the time between the first keypress and last key release). Correct sequences performed faster than the MT threshold (see below) were rewarded with one point. MTs that were 20% faster than the threshold was rewarded with three points. Incorrect presses or MTs exceeding the threshold resulted in zero points. At the end of each block, participants received feedback on their error rate, median MT, points obtained during the block, and total points obtained during the session. In order to motivate participants to continue to improve their performance, we adjusted the MT threshold by lowering it by 500 ms after each block in which the participants performed with an error rate of 15% or lower and had a median MT faster than the current threshold. This manipulation resulted in a stable overall error rate of 14.6%, SD: 2.6%. On 27% of trials, participants received one point, on 34% of trials three points.

2.2.4 Baseline study for measuring execution-level constraints

One of the aims of the study was to design specific ways of chunking a sequence that would induce either better or worse performance. We hypothesized that it would be advantageous to have chunk boundaries fall on transitions between fingers that are, based on execution-level constraints, executed slowly. We define execution-level constraints as factors arising from the neural control of movement, biomechanics, and characteristics of the keyboard device, independent of cognitive factors. To determine these constraints on finger transition speed – i.e., how fast participants can naturally execute each of the 25 possible two-finger transitions (e.g. 12,13, 25 etc.), we recruited seven participants (five females, ages: 21-27) for a 3-day study. None of the

participants that participated in this experiment participated in the later main experiment. Participants executed all possible two-finger transitions (e.g., 25) and three-finger transitions (e.g., 125), each eight times per day. Each sequence was presented twice in a row. Each day, participants completed eight blocks with 150 trials each. The setup, task, and feedback were the same as described above.

Because participants only had to plan and execute two or three finger presses, we assumed that cognitive constraints, chunking, or planning processes should not have limited performance. Thus, the average speed of these transitions can be taken as a characterization of the execution-level constraints of our specific task. The data from the 2-finger transitions revealed a clear pattern (**Figure 2.1b**), in which transitions between adjacent fingers (e.g. 12, 23, 32 etc.) could be executed on average 68.5 ms faster than finger repetitions (e.g. 55, 33, 22 etc.). We tested this difference by comparing the average speed of adjacent finger presses with the average speed of repetitions with a paired t-test ($t_{(6)} = 13.965$, $p = 8.404e\text{-}06$; **Figure 2.1b**). To press the same finger twice, the force applied to the key had to first exceed the press threshold, then go below the release threshold and then cross the press threshold again. This rapid alternation of forces takes time to produce. In contrast, for two adjacent fingers, the second finger press can be initiated (have already reached the press threshold but have not yet been registered) before the previous finger is released, making it easier to rapidly produce this force pattern.

The overall 5x5 pattern of inter-press intervals (IPIs) was stable across participants (average correlation $r = 0.689$) and days ($r = 0.894$), even though participants improved their overall speed from 157 ms on the first day to 114 ms on the third day. The same pattern was also apparent for the 3-finger transition data. If we broke up the 3-finger transitions into the constituent IPIs, the average pattern correlated with the 2-finger transition data with r= 0.913.

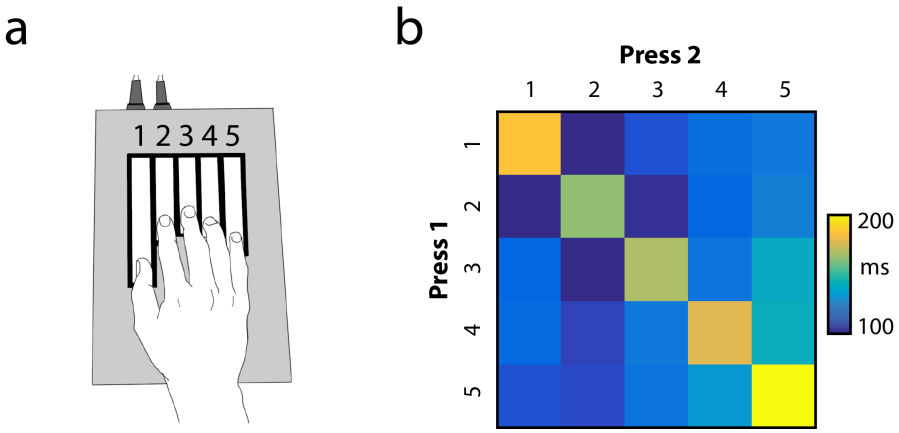


Figure 2.1 Apparatus & two-finger transition execution speed.
(a) Isometric keyboard-like device. Each key was associated with a number (these numbers were not shown to the participants but verbally explained). **(b)** Data from the independent baseline study in which participants performed all possible combinations of 2-digit transitions. Matrix indicates the median inter-press interval (IPI) to produce the transition between pairs of keypresses. Indicated values are means over seven participants.

2.2.5 Experimental design

To experimentally impose a particular way of chunking, we instructed participants in the experimental group to memorize and perform a set of 2-3 keypress chunks (**Figure 2.2a**). These chunks were later combined to form the training sequences (**Figure 2.2b**). Our goal was to impose beneficial or detrimental motor patterns on participants' performance. For this, we used the finding from the execution-level constraint baseline study that finger repetitions are performed slower than presses of adjacent fingers. We designed sequences such that they would include both fast transitions (runs e.g., 123 - 3-digit transition with two adjacent finger transitions that either are descending or ascending) and slow finger repetitions (e.g., 113). In the "aligned" chunk structure we inserted chunk boundaries such that they fell on difficult finger transitions, which were executed slowly. We hypothesized that participants could use the time required to perform these difficult finger transitions to recall the next chunk, which should benefit overall performance. In this chunk structure, the 3-digit "runs" (i.e. 123) were also kept intact within a chunk. We predicted that learning the sequence using this chunk structure would be beneficial to performance speed (**Figure 2.2c**). In the misaligned chunk structure, we placed chunk boundaries in a way that divided up fast finger transitions such as runs (e.g. 123), thereby breaking up parts of the sequence that could otherwise be performed very quickly. Adding chunk boundaries at easy finger transitions should lead to slower performance because these finger transitions now have to be used to recall the next chunk (which takes longer than executing the easy finger transitions). We hypothesized that this would hinder overall performance (**Figure 2.2c**). All participants practiced the same seven sequences (**Figure 2.2b**). Half of the participants in the experimental group were instructed with the aligned chunk structure for the first three sequences, and the misaligned chunk structure for the next three sequences (**Figure 2.2d**). For the other half of the participants, the assignment of sequences to aligned and misaligned was reversed. The last sequence (#) was neither misaligned or aligned under the two chunk structures, but was added to

ensure that each chunk occurred in at least two different sequences. The counterbalanced design (**Figure 2.2d**) allowed us to draw strong inferences about whether participants' performance was dictated by execution demands (which were identical across participants) or whether it was affected by the chunk structure imposed during the chunk instruction phase (which was different between the two chunk sets). We also included a control group that did not receive any explicit chunk instruction.

Every participant completed 15 training sessions in total (**Figure 2.2e**): one session per day across a 3-week period. Each session lasted approximately one hour, excluding the two initial sessions and the last session which each took two hours. Participants completed at least ten blocks of 28 trials per training day. Each block comprised four repetitions of each of the seven sequences.

Figure 2.2 Experimental design.

(a) Each participant learned 11 chunks associated with the chunk cues (A-K) from one of the chunk sets. **(b)** The seven 11-digit sequences that participants trained on. The vertical lines (not shown to the participants) indicate the chunk boundaries induced in training through the chunk set. Sequences were trained with an aligned (red) or misaligned (blue) chunk structure. **(c)** Example sequence containing a 3-digit run and two-digit repetitions. In the aligned structure, the chunk boundaries fell between repetitions, in the misaligned structure the chunk boundary broke up the run. **(d)** We counterbalanced across participants which sequences were practiced with which chunk structures. An additional control group was added who did not receive any chunk instruction **(e)** Experimental timeline depicting the training at each stage. In the instruction phase participants memorized chunks and sequences. In the optimization phase participants trained to perform these sequences as fast as possible from memory. In the last week of training, half of the participants were directly cued with the sequence, while the others performed the sequences from memory.

a

Chunk set 1	
Chunk	*Presses*
A	3 2
B	3 4
C	1 1 3
D	1 2 3
E	3 2 1
F	3 4 3
G	3 5 3
H	4 3 5
I	4 4 3
J	5 1 2
K	5 1 3

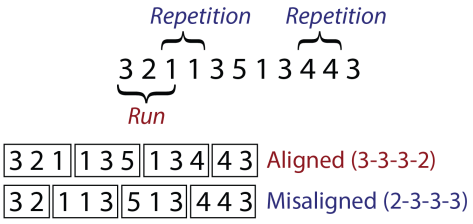
Chunk set 2	
Chunk	*Presses*
A	1 2
B	4 3
C	1 2 3
D	1 3 4
E	1 3 5
F	2 3 5
G	3 2 1
H	3 3 2
I	3 4 1
J	3 5 1
K	5 5 1

b

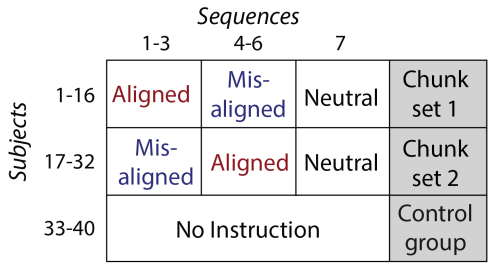
Sequence	Chunk set 1	Chunk set 2
?	1 2 3 | 5 1 3 | 3 2 1 | 3 4	1 2 | 3 5 1 | 3 3 2 | 1 3 4
+	4 3 5 | 5 1 3 | 3 2 1 | 3 4	4 3 | 5 5 1 | 3 3 2 | 1 3 4
%	4 3 5 | 5 1 2 | 3 5 3 | 3 2	4 3 | 5 5 1 | 2 3 5 | 3 3 2
$	3 2 | 1 1 3 | 5 1 2 | 3 4 3	3 2 1 | 1 3 5 | 1 2 3 | 4 3
&	3 2 | 1 1 3 | 5 1 3 | 4 4 3	3 2 1 | 1 3 5 | 1 3 4 | 4 3
@	3 4 | 1 1 3 | 5 1 3 | 4 4 3	3 4 1 | 1 3 5 | 1 3 4 | 4 3
#	3 4 | 1 2 3 | 5 1 2 | 3 4 3	3 4 1 | 2 3 5 | 1 2 3 | 4 3

\| Chunk Boundary — Aligned — Misaligned

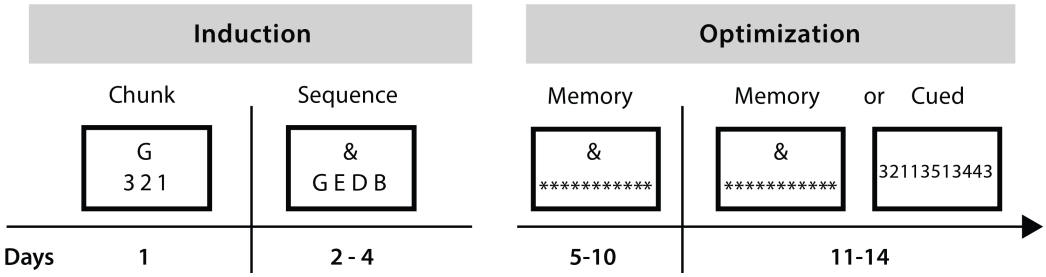
c



d



e



2.2.5.1 Days 1-4: Chunk instruction & initial sequence learning

For the experimental group, participants were pre-trained on one of the two chunk sets on the first day of training (**Figure 2.2a**). Each chunk was associated with a letter of the alphabet (A-K). Participants were explicitly told to learn this association. Each chunk was practiced twice in succession. On the first trial of each pair, the numbers corresponding to the finger presses where shown together with the letter indicating the chunk. On the second trial the numbers were replaced with stars, such that the participants had to recall the presses solely based on the letter. This trial order was reversed on every second block, such that participants had to first try to recall the sequence with the help of the letter, and then were shown both the letter and the numbers on the second trial. To ensure that participants had memorized the chunks we added recall blocks at the end of days 1 and 2. At the end of the first and second day, participants were asked to recall and type out the numbers corresponding to the presented letters as quickly and as accurately as possible (letters were randomly presented). At the end of day 2, participants could reliably produce the chunks from memory with an average accuracy of 92.7%.

On day 2, the experimental participants trained on the seven 11-press sequences. Each sequence was associated with a symbol (e.g. $; **Figure 2.2b**). Each symbol was presented twice in succession and participants had to perform the sequences from memory using the symbol cue on one trial or with the help of the chunk letters on the next trial. We tested participants' sequence knowledge with a recall block at the end of days 2-4. The first two participants did not perform the recall blocks. At the end of day 4, participants were able to recall all sequences from memory using the sequence cues with an accuracy of 93.1%.

In contrast, the control group did not receive any chunk training but instead trained directly on the seven 11-press sequences. On day 1 they were presented with the 11 digits corresponding to the 11-press sequences. We matched the amount of training across groups by ensuring that all participants were required to produce the same overall number of finger presses. On day 1,

the control participants were not aware that they would have to memorize the sequences later on. On days 2-4 they were instructed to memorize the sequences using the same symbolic sequence cues as the experimental groups and their memory was tested using recall blocks at the end of each day (Day 4: 90.2% accuracy). The rest of the experimental design was identical for all groups.

2.2.5.2 Days 5-10: Optimization - Memory Recall

On days 5-10 both experimental and control participants practiced exclusively on the eleven-press sequences using the symbolic cues. Chunks were no longer cued. Each sequence cue was presented twice in succession and participants had to recall the sequence from memory on both trials.

2.2.5.3 Days 11-14: Optimization - Memory recall or cued presentation

On the last four days of training half of the experimental participants performed the sequences from memory (as on days 5-10), while for the other half and for the control participants we removed the symbolic sequence cue and instead visually presented participants with the complete set of 11 digits that corresponded to the sequences (**Figure 2.2e**).

2.2.6 Statistical Analysis

We recorded and analyzed the force measured at each key. For each trial, we calculated movement time (MT, time between the first press and last release) and inter-press-intervals (IPIs; time between force peaks of two consecutive presses). All analyses were performed using custom-written code in MATLAB (The MathWorks) and the dataframe toolbox

(github.com/jdiedrichsen/dataframe). We excluded from our analyses trials that contained one or more incorrect presses, as well as trials with an MT or a press with an IPI three standard deviations above the mean calculated across all days and participants.

For the correlation analysis in **Figure 2.5**, we split the data for each day, participant and sequence in half (first vs. second half of each day) and calculated correlations of all possible pairs. We Fisher z-transformed the correlations before averaging and performing statistical tests. For plotting the correlations, we then inverse Fisher z-transformed the values.

The data were analyzed using mixed-effects analysis of variance (mixed ANOVA), Pearson's correlation and paired and one-sample t-tests. All t-tests were two-sided unless specified otherwise. A probability threshold of $p<0.05$ for the rejection of the null hypothesis was used for all statistical tests.

2.2.7 Probabilistic model for estimating chunk structure

To estimate participants' chunking behaviour from IPIs, we used an extended version of a Bayesian model of chunking behaviour, developed by Acuna and colleagues (2014). The algorithm uses a Hidden Markov Model to estimate the posterior probability that a specific chunk structure is present on a given trial. Here we used only the IPIs on correct trials, but not the error probability as in the original publication, as the probability of errors did not relate systematically to the imposed chunk structure early in learning.

As we had ten digit transitions, each of which could either coincide with a chunk boundary or not, we had to consider 2^{10}-1= 1023 possible chunk structures. Between trials, the hidden Markov process could either preserve the same chunk structure with probability *p* or switch to any other chunk structure with probability (1-*p*)/1022. The IPIs were modeled as a Gaussian random variable, with a

different mean and variance depending on whether the keypress transition was within or between chunks.

In contrast to Acuna and colleagues (2014), in which learning effects were removed in a preprocessing step using a single exponential, we modeled learning within our model using two separate exponential terms for the IPI mean. This captured the faster reduction in the between- compared to the within-chunk intervals (**Figure 2.3a**). The inclusion of separate learning curves for within- and between-chunk IPIs allowed us to estimate participants' chunk structure independently of changes in the overall performance speed (**Figure 2.6a**). This is an important advance over previous methods that used a constant cut-off value to distinguish between within- and between-chunk intervals. For these methods, faster performance would automatically decrease the number of chunk boundaries detected. To confirm that our algorithm did not show this bias, we simulated artificial data using parameter estimates for individual participants. We simulated sequences that switched between four different chunk structures, each of which contained four chunks. Even though IPIs decreased by about 300 ms with learning, the estimated average number of chunks remained stable across the entire simulated experiment (average distance to single chunk: 3.35 ~ 4 chunks and three boundaries).

We used an Expectation-Maximization (EM) algorithm to simultaneously estimate the posterior probability of each chunk structure for each trial, as well as the nine parameters of the model: three parameters each for the exponential curve for the within- and between-chunk IPIs, one variance parameter for each, and the transition probability *p (for implementation details, see* https://github.com/jdiedrichsen/chunk_inference).

As a preprocessing step, we regressed the IPIs for each participant against the average biomechanical profile, which was estimated as the average IPI profile for all possible two-digit presses from our biomechanical baseline experiment **(Figure 2.1b**). The fitted values were removed from the IPIs.

Removing temporal regularities that could be modeled with biomechanics alone should result in chunking estimates that more closely reflect cognitive and learning influences. Qualitatively comparable results were also obtained using the raw IPIs, without biomechanical factors removed.

2.2.8 Expected distance

We quantified how much participants changed their chunking behaviour over time by calculating the expected distance between their estimated chunk structure and a reference chunk structure. We defined the distance between two chunk structures, *d(i,j)*, as how many of the ten keypress transitions would have to change from a chunk boundary to a non-boundary (and vice versa) to transform one structure into the other (for an example, see **Figure 2.6b**). A distance of zero would indicate no change. The average distance between two randomly chosen chunk structures is five. Because chunk structures produced by participants on each trial were estimates, we calculated the expected distance. For this, we first calculated a 1023 X 1023 matrix containing the distances between any chunk structure *i*, and chunk structure *j*. From the posterior probability distribution, we could then derive how likely each of these chunk structure changes was, *p(i,j)*. The expected value of the distance was then calculated as

$$E(d) = \sum_{i=1}^{1023} \sum_{j=1}^{1023} p(i,j)d(i,j).$$

2.3 Results

Over 15 days we trained 32 participants to produce sequences of 11 isometric keypresses from memory on a keyboard-like device. Participants were rewarded with points for executing sequences as fast as possible while keeping the proportion of incorrect keypresses in each block of trials below 15%. We

maintained the participants' motivation by gradually decreasing the movement time (MT) threshold at which they received points.

We manipulated how participants memorized the sequences by splitting the sequences into several chunks, each composed of 2-3 keypresses. The aim was to test whether the different ways of chunking (hereafter "chunk structures") imposed through the chunk training in the instruction phase (Methods, **Figure 2.2b**) would affect performance optimization in the subsequent two weeks of training. Each sequence could be chunked in an aligned or misaligned fashion, predicted to lead to beneficial or detrimental performance respectively (Methods, **Figure 2.2c**). All participants practiced the same seven sequences but differed in the chunking instructions they received for each sequence.

2.3.1 Chunk instruction induces a stable movement pattern

To assess whether the imposed chunk structures influenced participants' motor behaviour, we examined inter-press time intervals (IPIs). An increased IPI is commonly taken as a sign of a chunk boundary, as the cognitive processes (memory recall, action selection) involved in switching from one chunk to another require additional time (Verwey, 1999; Verwey et al., 2010). Hence, we would expect our participants to exhibit shorter IPIs between keypresses that belonged to a chunk imposed during day 1 (within-chunk IPIs) and larger IPIs for the boundaries between chunks (between-chunk IPIs). For this analysis, we pooled the data from all sequences irrespective of instruction (misaligned vs. aligned). We indeed found significantly longer between-chunk IPIs compared to within-chunk IPIs in the first few days of training (**Figure 2.3a**: days 2-4: $t_{(31)} = 7.728$, $p = 5.098e\text{-}09$), suggesting that our manipulation was successful in inducing a temporally specific pattern of keypresses.

In the optimization phase, we ceased to cue sequences using the alphabetic letters associated with the chunks. Instead, participants were asked to

recall the entire 11-keypress sequences from memory in response to symbolic sequence cues (e.g. “$”). Across days 5-10, the within and between-chunk IPIs were still significantly different from each other; $t_{(31)} = 7.165$, $p = 2.351e\text{-}08$ (**Figure 2.3a**). This difference cannot be attributed to differences in performance difficulty of the finger transitions, as the within-chunk IPIs for one half of the participants were the between-chunk IPIs for the other half and vice versa (**Figure 2.2b**). IPIs that were within-chunk for all participants (e.g., the first and last IPI of a sequence) were excluded from this analysis.

In the last four days of training, we tested whether the slower IPIs at chunk boundaries were due to the fact that the sequences needed to be recalled from memory. Half of the participants continued to perform the sequences from memory, whereas the other half were cued using the numbers that indicated the necessary keypresses (**Figure 2.2e**), therefore removing any memory recall demands. Both the memory ($t_{(15)} = 4.865$, $p = 2.059e\text{-}04$, **Figure 2.3b**) and the cued subgroup ($t_{(15)} = 3.403$, $p = 0.004$) showed a significant difference between the within- and between-chunk IPIs. There was no reliable difference between the two subgroups in this effect ($t_{(30)} = -0.749$, $p = 0.460$). Thus, removing the requirement for memory recall did not abolish chunking. Because none of the subsequent analyses showed any significant difference between the two subgroups, we will report their combined results for the remainder of the article.

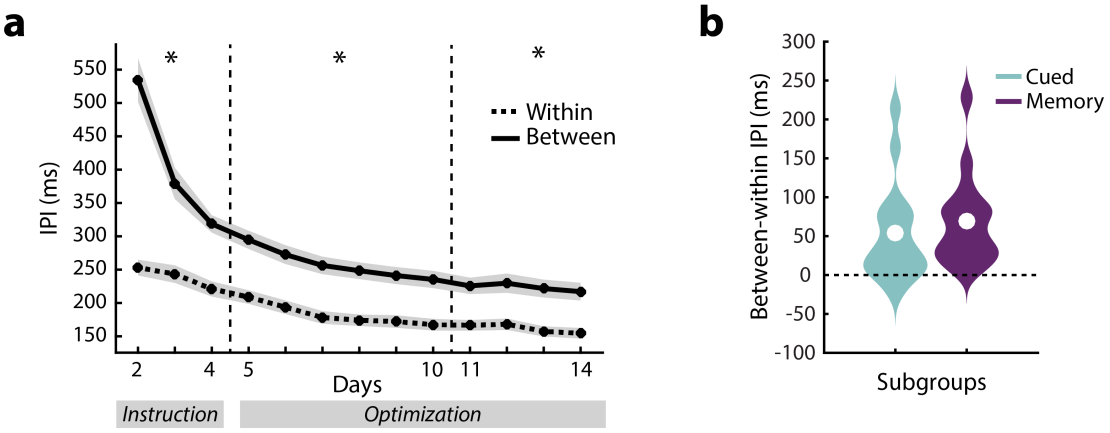


Figure 2.3 Within- vs. between-chunk inter-press intervals (IPIs).
(a) Time course of IPIs that were within an instructed chunk (dashed line), or on the boundary between chunks (solid line). Asterisks indicate significant differences between average within- and between-chunk IPIs in the corresponding week (separated by dashed lines). Shaded area denotes between-subject standard error. **(b)** Difference of between- and within-chunk IPIs in the last week of training, split by whether participants had to recall the sequences from memory or were cued with the sequence numbers. Violin plots indicate distribution of individual participants, white circles indicate means.

2.3.2 Misaligned chunk structure impairs performance

We then asked whether the two types of chunk instructions that were used for each sequence (counterbalanced across participants) would lead to measurable differences in performance. We designed chunk structures that were either aligned or misaligned with the basic execution-level constraints (see Methods), and predicted that these structures would either improve or impede performance. Each experimental participant learned three of the seven sequences with a misaligned chunk structure and three sequences with an aligned chunk structure, with the assignment counterbalanced across participants (**Figure 2.2d**). Therefore, all participants practiced the same seven sequences, but differed in which chunk instructions they received. This counterbalanced design allowed us to compare execution speed between aligned and misaligned sequences within each participant.

To test our prediction that training with the misaligned chunk structure would lead to poorer performance, we measured participants' movement time (MT) by estimating the time between the first finger press and the last finger release. For each participant we then calculated the difference in average speed between the aligned and the misaligned instructed sequences. As predicted, in the instruction phase, sequences instructed with the misaligned chunk structure were performed slower than the sequences instructed with the aligned chunk structure (**Figure 2.4a**) one-sample t-test: $t_{(31)} = 2.693$, $p = 0.006$. Hence, we were not only able to manipulate how participants performed a sequence, but also how well they could perform it.

Next, we wanted to examine what factors influenced the difference in speed we observed. To determine how beneficial it was to have a finger run (three adjacent presses in either descending or ascending order, e.g. 123) preserved within a chunk, rather than separated by a chunk boundary, we selected all IPIs that could be either within or between a chunk (excluding the IPIs that were within-chunk for both aligned and misaligned structures). For the within-chunk IPIs, we compared the average IPI for transitions that occurred in a

run (e.g. between 1&2 and 2&3), to the average IPI for transitions outside of a run (e.g. 2&4 or 5&1). This gives us an idea of how beneficial it is for a finger run to be present within a chunk compared to when there is no run present. We then compared this measurement to how advantageous a run is when it is separated by a chunk boundary. In other words, we compared the advantage of having a finger run within a chunk to having a finger run that is distributed across chunks. We found a significant advantage of 28.6 ms (SD 44.6; one-sided t-test: $t_{(31)}$ = 3.624, p = 5.137e-4). Similarly, we calculated the cost of a finger repetition within a chunk, as compared to the cost of a finger repetition between chunks and found an average difference of 16 ms (SD 68.1), a non-significant difference (one-sided t-test: $t_{(31)}$ = 1.331, p = 0.097). An additional factor that influenced participants' speed was whether the 2-digit chunk was placed in the beginning (misaligned) or the end of the sequence (aligned). We evaluated this factor by averaging the second and second-to-last IPI in each sequence, as one of them was within-chunk and one was between-chunk for each sequence. This comparison showed an significant advantage of 24.7 ms (SD 60.0) for the aligned chunk structure (one-sided t-test: $t_{(31)}$ = 2.330, p = 0.013). These results suggest that multiple factors led to an MT advantage for sequences that were instructed with an aligned vs. misaligned chunk structure.

The difference in MT we found in the first week was maintained in the second week of training (days 5-10: $t_{(31)}$ = 2.313, p = 0.014). However, this speed difference was no longer statistically reliable in the last four days of training (days 11-14: $t_{(31)}$ = 0.764, p = 0.225). This suggests that participants ultimately were able to overcome the performance detriment that we imposed through the initial chunk instructions.

To determine whether receiving the aligned chunk instruction was more beneficial to performance than not receiving a chunk instruction at all, we tested an additional control group. This group did not have to explicitly learn chunks, but rather trained on the entire sequences from the beginning (see Methods for details). We compared the performance of this group to the experimental group

for days 5-10, during which all groups had to perform the sequences from memory. During these days, the control group performed on average 63.5 ms (standard error 223.2 ms) slower than the experimental group on the aligned sequences, and nearly identical (0.5 ms slower, SE 215.3 ms) compared to the performance of the experimental group on the misaligned sequences. However, neither of these contrasts reached statistical significance (Aligned vs. control: $t_{(38)} = -0.285$, $p = 0.778$; misaligned vs. control: $t_{(38)} = -0.002$, $p = 0.998$).

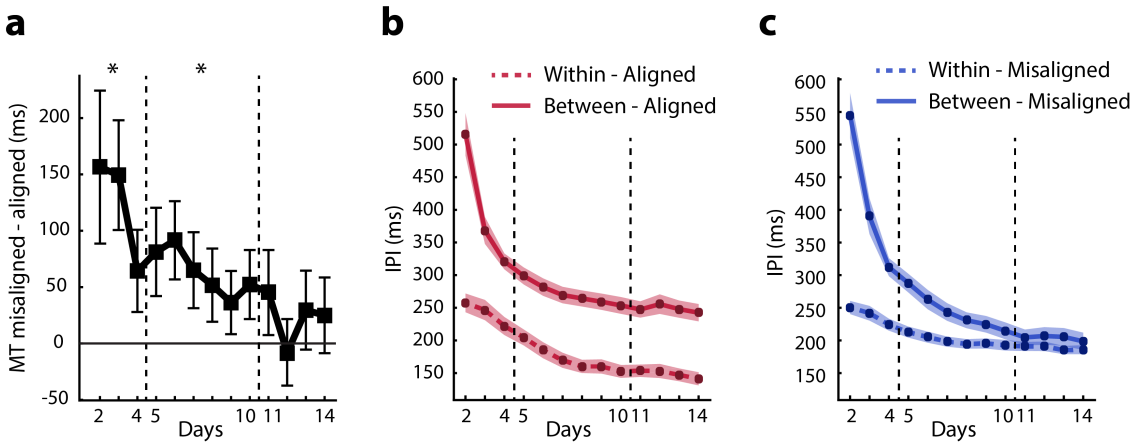


Figure 2.4. Change in chunk structure and performance for aligned and misaligned instructed sequences.

(a) Differences in movement time (MT) between sequences instructed with an aligned or misaligned chunk structure. Asterisk indicates a significant difference from zero (no difference). **(b)** Within- or between-chunk IPIs across training days for the sequences instructed with the aligned chunk structure. **(c)** Within- or between-chunk IPIs across training days for the sequences instructed with the misaligned chunk structure. Error bars denote between-subject standard error.

2.3.3 Misaligned chunk structure is changed more rapidly

To investigate how participants overcame the detrimental influence of the misaligned chunk structure, we separated the IPI analysis (**Figure 2.3a**) by whether the intervals came from sequences that were instructed using an aligned or misaligned structure. The difference between within- and between-chunk IPIs for sequences instructed with the aligned chunk structure was stable over the entire training period (**Figure 2.4b**). In contrast, for the misaligned structure, the difference between the within- and between-chunk IPIs started to disappear late in learning (**Figure 2.4c**). The three-way day x within/between x aligned/misaligned interaction was significant ($F_{(12,372)}$ = 19.790, p = 1e-16). Thus, participants diverged from the misaligned chunk structure while maintaining the aligned chunk structure.

To understand these changes in more detail, we investigated the entire pattern of IPIs produced by the participants for each sequence. In a first analysis we correlated the participants' IPI pattern of each day to the pattern produced on day 2 (**Figure 2.5a**, see methods for details). This analysis shows how far participants diverged from their initial chunking pattern with training. The comparison between the aligned and misaligned instructed sequences confirmed our previous observation that participants diverged more from the misaligned instruction (Day X Instruction: $F_{(11,330)}$ = 4.348= p= 4.352e-06). The analysis also demonstrates that the control group significantly diverged from their second day IPI pattern with training (Day: $F_{(11,77)}$ = 30.209, p <0.0001).

Importantly, our data shows that this drift was not due to participants becoming more variable in their performance. To investigate the stability of the temporal structure within each day, participant, and sequence, we correlated the average IPI patterns across the first half and second half of each day. To test for a systematic change of stability across training, we fitted a linear regression separately to each participants' correlation results and compared the resulting slope values to zero. We found that within-subject correlations increased over the course of training for the aligned instructed sequences ($t_{(31)}$ = 4.204, p = 3.071e-

05) as well as for the control group ($t_{(31)}$ = 2.874, p = 0.024, **Figure 2.5b**). For the misaligned instructed sequences the increase failed to reach significance ($t_{(31)}$ = 1.9744, p = 0.0573, **Figure 2.5b**). We also found that the chunking pattern for the misaligned instructed sequences was less stable than for the aligned instructed sequences ($t_{(31)}$ = 2.952, p = 0.006). Overall, however, correlations were very high (r>0.9), showing that participant adopted a relatively stable temporal structure for each sequence.

Given that participants converged on a stable IPI pattern for each sequence, we asked whether this pattern was the same across participants, or whether individuals found idiosyncratic solutions. To explore this question, we again used the average IPI pattern for each half day, but now correlated these patterns with those of any of the other participants. This approach enabled us to directly compare how similar two participants performed the same sequence in a session (between-subject correlation), with how consistent a single participant performed that same sequence (within-subject correlation). For the experimental group, we found that between-subject correlation (**Figure 2.5c**) was substantially lower than the within-subject correlation ($t_{(31)}$ = 19.664, p <0.0001) at the end of training (day 14). This suggests that participants adopted chunk structures at the end of training that were stable, but quite different across participants. This was especially true for the misaligned instructed sequences, which showed a lower between-subject correlation than the aligned instructed sequences on the last day of training ($t_{(31)}$ = -8.211, p = 2.834e-09, **Figure 2.5b**). Similarly, the control group also shows much higher within-subject than between-subject of the IPI patterns ($t_{(7)}$ = -19.119, p = 2.666e-07). Together, these results show that participants, independent of chunk instruction, changed their IPI patterns systematically over training, converging on idiosyncratic, but individually stable temporal patterns of performance.

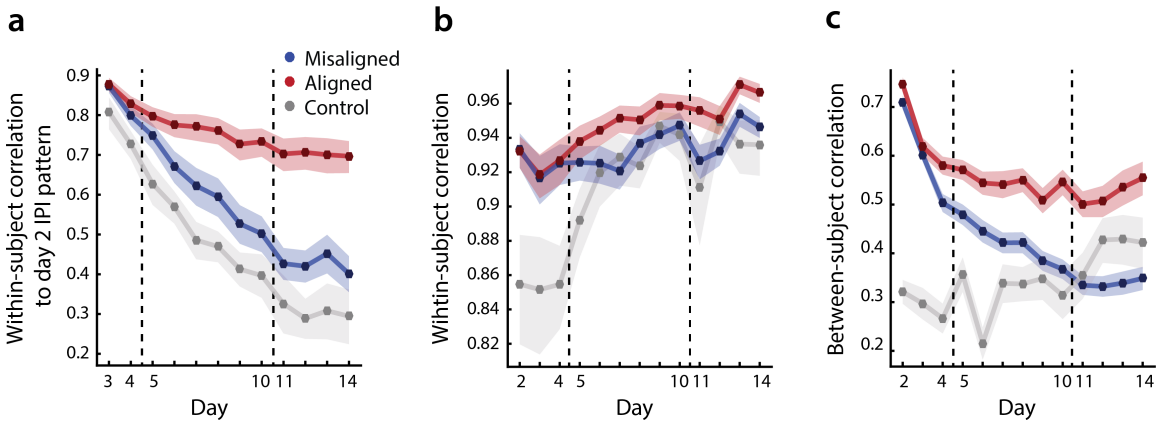


Figure 2.5 Changes of IPI pattern across training.

(a) Within-subject correlation of IPI pattern of day 2 with the IPI pattern of each subsequent day, averaged across the first and second half of blocks. Correlation separated for misaligned and aligned instructed sequences and control group. **(b)** Within-subject IPI pattern per day between first and second half of data. **(c)** Between-subject IPI pattern separated by instruction across days.

2.3.4 Bayesian model of chunk behaviour

To get a more detailed understanding of how participants changed their chunk structure across training, we used a Bayesian model to estimate the probability of each possible chunk structure given the observed series of IPIs on a trial-by-trial basis (Acuna et al., 2014). The state variable in this Hidden Markov Model represents which of the 1023 possible chunk structures is present on each trial. Using an expectation-maximization (EM) algorithm (Dempster et al., 1977; Welch, 2003), we simultaneously estimated the nine free parameters of the model (for details see Methods), and the posterior probability for each possible chunk structure on each trial. We accounted for the effects of biomechanical difficulty by regressing out the patterns of IPIs across finger transitions predicted from our biomechanical dataset (**Figure 2.1b**) before modeling. Importantly, our model could capture separate learning-related changes to the within- and between-chunk intervals (**Figure 2.6a**). Our method, therefore, allowed us to estimate participants' chunk structure independently of the overall speed of performance.

Figure 2.6b shows two examples of individual participants and sequences. In the first panel, the participant chunked the sequence according to the initial instructions at first, then inserted one or two additional chunk boundaries, and at the end of training performed the sequence as a single chunk. In comparison, the other participant maintained the instructed chunk structure for most of the training period.

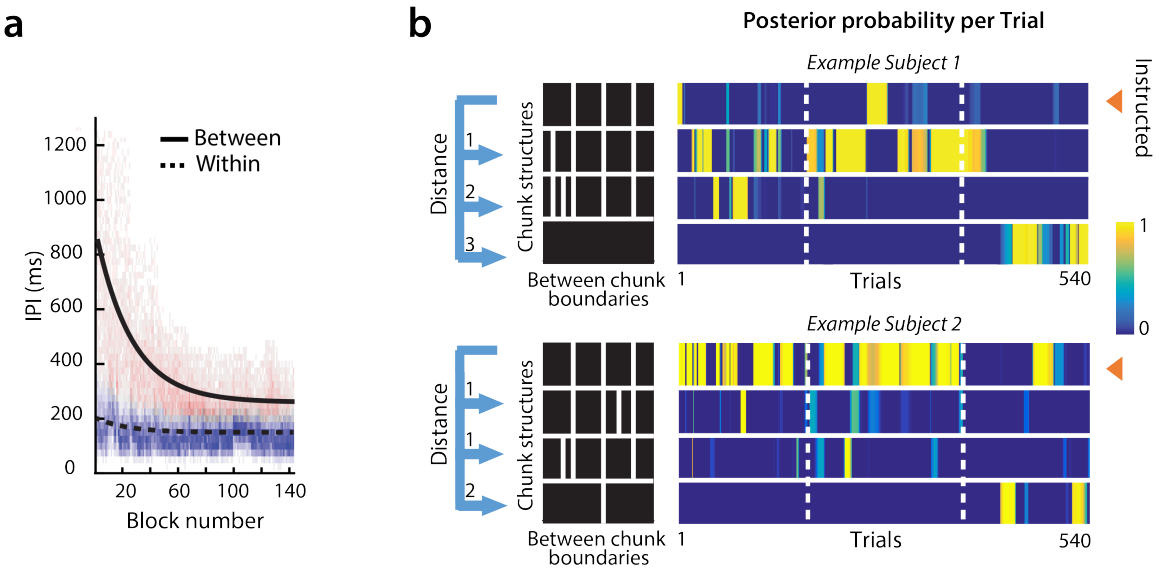


Figure 2.6 Probabilistic chunking model fitted to example participant data. **(a)** The change of within- and between-chunk IPIs were modeled using two separate exponential functions across training. The density plot shows individual IPIs, with the color indicating the probability of a between- (pink) or within-chunk interval (blue). **(b)** Posterior probability for two example participants (for one sequence per participant) over the course of the experiment. Only the four most likely chunk structures out of the 1023 possible structures are shown. The color scale indicates the posterior probability of a given chunk structure for each trial - with yellow indicating higher probabilities. The dashed vertical lines indicate the boundaries between training phases (Days 2-4; 5-10 & 11-14). The black box (left) indicates the chunk boundaries as white lines within the 11-press sequence (maximal 10 boundaries) for the chosen chunk structures. The first row indicates the instructed chunk structure (arrow). The other three rows illustrate other chunk structures that were highly probable at some point during the experiment. The distance measure expresses how many chunks need to be added or removed to transform one structure (in this case the instructed chunk structure) into the other.

To characterize changes in chunk structure over training we defined a metric that quantified the difference between any two chunking structures. The metric is based on counting the number of chunk boundaries that differ, in other words, the number of chunks that would need to be split or merged to transform one chunk structure into the other (**Figure 2.6b** - distance). We then used this measure to calculate, on each trial, the distance between the chunk structure estimated for the participant and three reference structures of interest: (1) the aligned-, (2) misaligned, and (3) a structure that consisted of a single chunk. These distances defined a coordinate system that enabled us to visualize changes in chunk structure over training. We then projected participants' estimated chunk structures into this space (**Figure 2.7a**). On the horizontal axis is the expected distance of participants' chunk structure to the single-chunk structure. Given our definition of distance, this measure simply counts the number of chunk boundaries. The vertical axis indicates how close the estimated chunk structure is to the aligned and misaligned chunk structure, respectively.

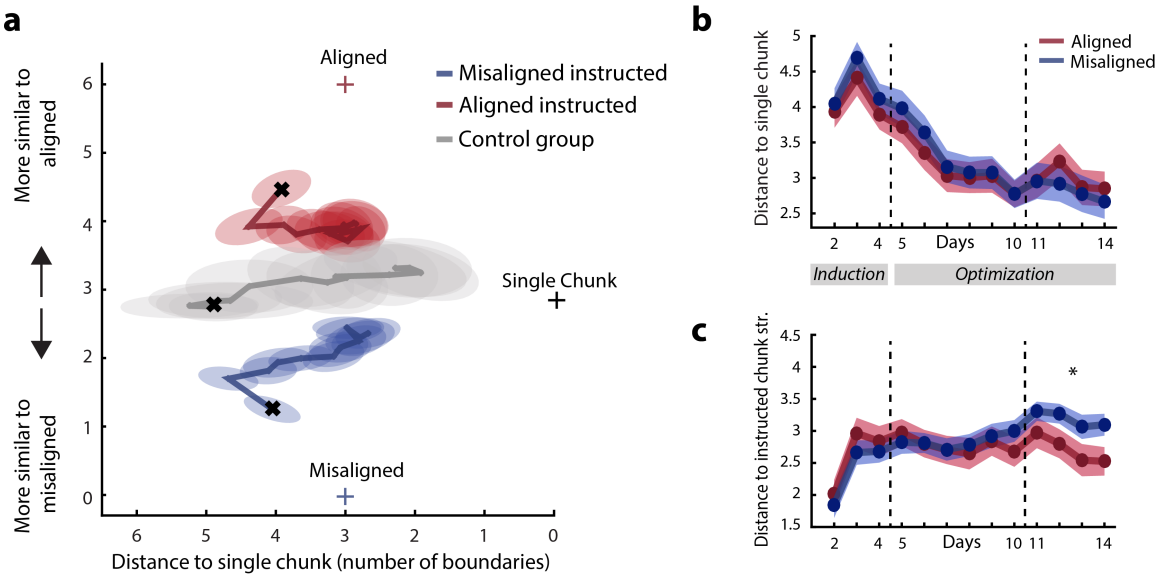


Figure 2.7. Changes in chunk structure with learning.

(a) The average chunk structure over 13 days of practice for aligned (red) and misaligned (blue) instructed sequences for the experimental participants. The results of the control group are shown in grey. The horizontal axis represents the distance to the single-chunk structure, i.e., the number of chunk boundaries. The vertical axis shows the distance to the aligned or misaligned chunk structure. The crosses indicate the positions of the three reference structures (aligned, misaligned and single). Ellipses denote the between-subject standard error. **(b)** Average distance of participants' chunk structure to the instructed chunk structure. **(c)** Distance to the single chunk structure across days.

2.3.5 Participants abandoned the misaligned faster than aligned chunk structure

First, we wanted to compare the findings from our IPI analyses with the results from the modeling approach. Consistent with our IPI analysis (**Figure 2.4b**), we observed that participants abandoned the instructed misaligned chunk structure to a greater degree than the aligned chunk structure (Day x Instruction interaction: $F_{(12,372)} = 5.610$, $p < 1e\text{-}16$). In the last four days of training, sequences with the misaligned chunk structure were more dissimilar to the instructed chunk structure than sequences with an aligned chunk structure: $t_{(31)} = 2.294$, $p = 0.029$ (**Figure 2.7b**). Additionally, we found a significant Day x Instruction interaction ($F_{(12,372)} = 2.215$, $p = 0.011$) for the distance to a single chunk (**Figure 2.7c**), suggesting a stronger tendency towards performing a sequence as a single chunk when trained on the misaligned chunk structure. Together these results indicate that participants changed their chunking behaviour more readily for sequences that were trained using the misaligned chunk structure than when trained using the aligned chunk structure.

Despite the divergence from the misaligned chunk structure with training, our analysis also revealed that participants did not overcome the influence of the instruction completely. In the third week, sequences trained with a misaligned chunk structure were still performed using a chunk structure that was closer to the misaligned structure than to the aligned structure ($t_{(31)} = 6.962$, $p < 1e\text{-}16$). This shows that training with a misaligned chunk structure had a lasting influence on participants' motor behaviour.

Interestingly, on the first day, the control group performed the sequences closer to the misaligned chunk structure than to the aligned chunk structure ($t_{(7)} = -2.799$, $p = 0.027$). With training, participants then moved closer to the aligned chunk structure, as indicated by a significant change in the difference between the distance to the aligned and misaligned chunk structure across days ($F_{(12,84)} = 5.303$, $p < 1e\text{-}16$).

2.3.6 Movement towards a single chunk structure

Previous literature has suggested that with training, participants group smaller chunks together to form new larger chunks (Kuriyama et al., 2004; Ramkumar et al., 2016; Sakai et al., 2003; Song and Cohen, 2014; Verstynen et al., 2012; Verwey, 1996; Wymbs et al., 2012), a process that may help to improve performance (Abrahamse et al., 2013; Ramkumar et al., 2016; Verwey, 2001, 1999; Verwey et al., 2010; Verwey and Wright, 2014). However, in nearly all previous studies the estimated number of chunks is biased by the overall movement speed. As verified by simulations (see Methods), our probabilistic model was able to disambiguate the two factors. We estimated the number of chunk boundaries for each participant averaged across sequences. On the second day, participants separated sequences into more chunks than the four chunks we instructed (**Figure 2.7c**, $t_{(31)} = 4.224$, $p = 0.0002$). This tendency continued on day 3, on which participants tended to subdivide the sequences into even smaller chunks (day 2 vs. 3: $t_{(31)} = 2.023$, $p = 0.052$). After day three the number of chunk boundaries decreased as shown by a significant effect of day in a repeated measures ANOVA ($F_{(11,341)} = 11.710$, $p < 1e\text{-}16$). However, even in the last phase of training, participants performed the sequences with an average of 2.9 chunk boundaries (we instructed three chunk boundaries). Thus, while there was a clear tendency towards merging chunks after an initial increase, participants did not perform the sequence as a single chunk, even after three weeks of practice.

Similar to the experimental groups, the control group initially subdivided the sequences into small chunks and then slowly combined them into larger chunks. The distance to a single chunk structure decreased significantly over days ($F_{(12,84)} = 17.977$, $p < 1e\text{-}16$, **Figure 2.7a**), and reached a level that was not statistically different from the experimental participants on the last day of training ($t_{(38)} = -0.940$, $p = 0.353$).

2.3.7 Idiosyncratic chunk structures at the end of training and their importance to performance

Finally, we analyzed how the final chunk structure that participants adopted for each sequence influenced their performance after three weeks of training. We visualized this relationship by plotting the chunk structure for each sequence and participant in the 2-dimensional space defined in earlier **Figure 2.7a**, with the corresponding average MT indicated by the size of the symbol (**Figure 2.8**).

The first insight is that participants used quite diverse chunk structures. To show that this is not due to within-subject variability of performance, we compared participants' within-subject variation in IPI patterns for each sequence across even and odd trials (in the last three days of training) to the between-subject variation in IPI patterns for each sequence. We found that the between-subject variability was much higher than the within-subject variability ($t_{(31)}$ = 36.130, $p < 1e\text{-}16$). Similar to the findings of the IPI analyses, this shows that participants developed their own, idiosyncratic way of chunking each sequence, which is not fully dictated by the biomechanical requirements of the sequence. With this result in mind, we asked whether these individual differences relate to differences in final performance.

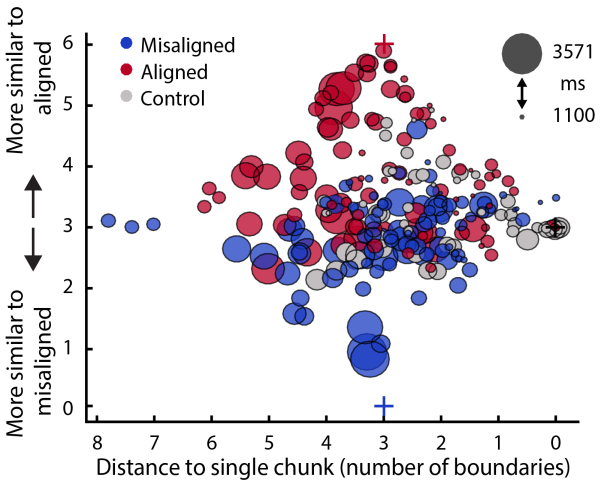


Figure 2.8 Relationship between chunking and speed (days 11-14).
The x-axis indicates the distance to a single chunk and the y-axis the relative distance to the two instructed chunk structures. Each data point indicates the average chunk structure and MT of a single sequence and participant in the last four days of training. The diameter of each circle represents the MT with larger circles indicating slower performance.

Figure 2.8 suggests, that performance was better for sequences that were closer to the aligned chunk structure. To statistically test whether this finding holds true within each individual, we regressed the MT for six sequences for each participant in the last four days of training against the corresponding distance to the aligned chunk structure. On average the individual slopes were significantly greater than zero, both for the experimental (**Figure 2.9a**; $t_{(31)}$ = 2.220, p = 0.017), and control group (**Figure 2.9b**, $t_{(7)}$ = 2.720, p = 0.015). Thus, finding a better way of chunking (for the same number of chunk boundaries) improved performance.

Secondly, **Figure 2.8** also suggests, that performing the sequence with a reduced number of chunks is beneficial for performance. We regressed the MT for six sequences (last four days) against the corresponding distance to the single chunk structure to (**Figure 2.9c**). The majority of the participants showed a positive relationship between the number of chunks and MT: a one-sample t-test indicated that the individual slopes were significantly greater than zero ($t_{(31)}$ = 6.104, p = 4.560e-07). This relationship was also found for the control participants (**Figure 2.9d**, $t_{(7)}$ = 3.429, p = 0.006). Thus, performing the sequences with fewer chunks led to better performance. Note that for both analyses, the chunk structure can be determined independently from the overall performance criterion (MT, see Methods).

Overall, these results suggest that the two optimization processes - joining chunks and aligning the remaining chunk boundaries with biomechanical constraints - positively influenced participants' ultimate performance. Sequences for which participants could not develop a better way of chunking were performed substantially slower.

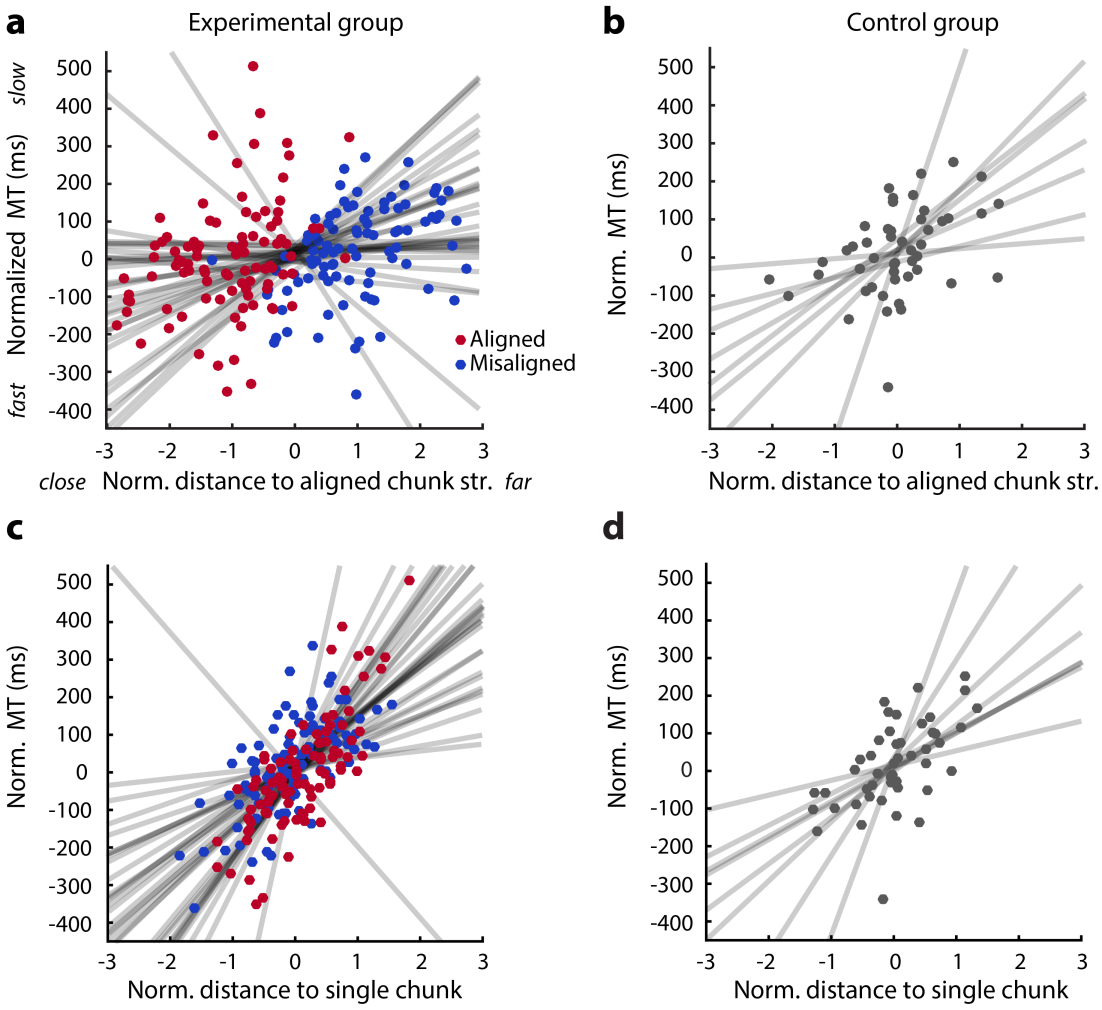


Figure 2.9 Relationship between the distance to the aligned/single chunk structure and MT.

(a) Scatterplot between the normalized (per participant) distance to the aligned chunk structure and normalized MT in the last four days of practice. A separate regression line is fitted to the six sequences for each participant. Red dots indicate sequences with aligned instructions, blue dots sequences with misaligned chunking instructions. **(b)** Same as a but for the control group. **(c&d)** same as a & b but for the normalized distance to a single chunk.

2.4 Discussion

In this study, we utilized chunking as a tool to investigate the role of instructions on skill learning. We influenced the structure of the initial declarative sequence representation by manipulating how participants memorized them (Park et al., 2004). Moreover, by experimentally imposing two different chunk structures on the same physical sequence, one that was beneficial and one that was detrimental to performance, we could make causal inferences about the effects of chunking on motor skill development. This is an important advance over previous observational studies (Ramkumar et al., 2016; Wright et al., 2010; Wymbs et al., 2012), which did not experimentally control how participants chose to chunk the sequences.

We report four main results. First, consistent with previous studies (de Kleine et al., 2009; Verwey et al., 2010, 2009; Verwey and Dronkert, 1996), our data demonstrate that a stable chunking pattern can be induced through cognitive manipulations during the initial stages of sequence learning. Importantly, participants did not completely overcome this imposed chunk structure and the chunking structure remained stable, even when the task changed from a memory-guided to a stimulus-guided task. Thus, the initial chunk instructions led to the formation of specific movement patterns.

Second, we were able to induce chunking patterns that differentially affected participants' performance. To do so, we designed two different ways of instructing the sequence, one aligned and the other misaligned with execution-level constraints that were identified using a separate participant population. Using this manipulation, we were able to induce a performance difference in the beginning of practice, which was still observed during the second week of practice but disappeared in the last week. While these results clearly show that instructions can systematically impact performance, the comparison to participants that trained without explicit chunking instructions does not allow firm conclusions on whether this difference was caused by the aligned instruction

facilitating performance, the misaligned instruction impeding performance, or both.

Third, more detailed analyses of the inter-press interval patterns showed that participants followed the beneficial chunk instructions throughout the entire training period, but changed their chunking pattern for the misaligned instructed sequences. We also demonstrate that participants did not all converge on the same chunking pattern after abandoning the misaligned instructions, but rather found an idiosyncratic chunking structure for each sequence. These solutions differed across participants, but were relatively stable within each participant at the end of training. Similar observations were made for the control group. The stabilization of IPI patterns that we observed over the course of training can be compared to the development of an invariant temporal and spectral structure in bird-song, a process that has been termed “crystallization” (Brainard and Doupe, 2002).

Finally, we identified two ways in which participants overcame the limitation induced by the bad habit. After initially breaking up the instructed sequences into five chunks on average, participants then joined chunks together, and by doing so, decreasing the amount of additional time spent on chunk boundaries. While previous research has suggested that the size of chunks increases with training, these findings were usually conflated with the overall speed of the action (Solopchuk et al., 2016; Song and Cohen, 2014; Wymbs et al., 2012). Using a Bayesian model to assess chunk structure independent of performance, we demonstrated a positive relationship between chunk concatenation and execution speed, both in the experimental as well as in the control group that developed a chunking strategy without explicit instructions. However, our results also indicate that participants did not merge all sequences into a single chunk after three weeks of training, but on average subdivided each sequence into 3-4 chunks. This suggests that the number of motor actions that can be joined in a single chunk may be limited (Langan and Seidler, 2011; Ramkumar et al., 2016; Verwey et al., 2002; Verwey and Eikelboom, 2003).

Furthermore, we found that participants also optimized performance by rearranging chunk boundaries in a biomechanically efficient manner. Consistent with our prediction based on the difficulty of individual digit transitions, placing chunk boundaries at digit transitions that take more time to execute and combining finger presses that are adjacent resulted in faster performance for the full sequence. This optimization process was also observable in the control group that memorized and practiced sequences on their own terms. Conversely, we observed that sequences that were not chunked in line with these strategies were performed slower. Therefore, if a more beneficial way of chunking was not found, participants still produced sequences using longer movement times, suggesting that other learning mechanisms did not fully make up for a persistent motor habit. Considering that participants' behaviour became highly invariant in the last week of practice, we predict that some motor habit will remain and continue to influence participants' performance even after prolonged training.

In many motor tasks, there are numerous strategies and processes that can lead to excellent performance (Verstynen et al., 2012; Verwey et al., 2010). Examining **Figure 2.8**, one can observe that the shortest MTs were achieved anywhere in the space between the aligned and single chunk structure. Occasionally, good performance was also reached in other locations in chunk space. Our analysis showed that participants adopted quite idiosyncratic chunk structures for each sequence at the end of training. This suggests that there is considerable inter-individual variability in which technique works best for reaching a high level of performance. Part of these differences may reflect biomechanical variation across participants, leading to slightly different optimal solutions. Alternatively, these differences may be learning-related. A number of ways of chunking may work approximately equally well, such that the cost of changing an established habit may outweigh the small benefit that could be gained from changing the structure. A similar observation can be made in sports, where even top-ranked athletes use slightly different techniques to reach similar levels of performance.

An alternative interpretation of the data is that with training participants' temporal inter-press interval patterns are primarily driven by execution-level constraints of the sequences rather than by chunking. This would mean that chunking is abolished with training and the remaining regularities we observe are due to physical constraints (i.e., how fast can each finger transition be executed). Some aspects of our findings, however, speak against this possibility. Execution level constraints have a relatively high (r = 0.689) inter-subject correlation (see baseline study results), and we would have expected a similarly high correlation for the IPI patterns. Our finding that the between-subject IPI correlation is substantially lower and also differed across chunk instructions, therefore speaks against this possibility. This line of reasoning would also suggest that participants that did not receive any explicit chunk instructions (the control group) developed stable chunking patterns with training, supporting claims by previous studies (Ramkumar et al., 2016; Wright et al., 2010; Wymbs et al., 2012).

The characteristics of the stable motor patterns we observed make them similar to "habits". Habits are defined as highly entrenched behavioural pattern that resists change through retraining (Ashby et al., 2003; Dezfouli and Balleine, 2012; Dolan and Dayan, 2013; Graybiel, 2008; Graybiel and Grafton, 2015; Hardwick et al., 2019; Hélie et al., 2010; Jager, 2003; Robbins and Costa, 2017; Seger and Spiering, 2011; Smith and Graybiel, 2013a), even if they have become maladaptive. Most papers on habits (Jog et al., 1999; Robbins and Costa, 2017; Smith et al., 2014; Smith and Graybiel, 2016; Wickens et al., 2007) have focused on habits in the context of action selection – i.e. choosing *what* action to perform. In contrast, our experiment addresses the question of habits in motor performance – i.e. habits that influence *how* to perform a chosen action. For example, a tennis player could be influenced by a habitual pattern in action selection, whereby they always choose a forehand over a backhand to return a serve. At the same time, they could be influenced by a motor habit, whereby they execute the forehand without rotating their hips. In support of this idea, we showed that we could induce a stable performance pattern that can be observed even after weeks of training, that these performance patterns crystallized over

the course of training, and that changes in task demands did not lead to behavioural modifications. Therefore, we believe that studying chunking can provide valuable insights into the neural systems underlying motor habits. Indeed, it has recently been suggested that chunking plays an integral role in the formation and expression of habits (Dezfouli et al., 2014; Graybiel, 2008) and is neurally represented in the dorsal lateral striatum as action “start and stop signals” (Barnes et al., 2005; Graybiel, 1998; Jin et al., 2014; Smith et al., 2014; Smith and Graybiel, 2013b).

The establishment of a paradigm which allows us to not only cognitively influence participant movement patterns, but also influence their behavioural impact on performance, will enable us to explore ways to encourage learners to change their current movement pattern, especially if it is disadvantageous. While our deliberate attempt at modifying participants’ behaviour by changing the task from a memory-based to a stimulus-based task was ultimately not successful, there are many other techniques that could be used. In many disciplines, teachers have developed ways to help students overcome habits. Such techniques often relate to changing context, speed or overall execution (De Souza, 2020, 2017; Ito, 2020).

In conclusion, we were able to use a sequence chunking paradigm to impose specific movement patterns on participants’ behaviour that in turn impacted their mental representation. We found that these movement patterns were stable across three weeks of training. Furthermore, by aligning the imposed chunking patterns with beneficial or detrimental finger transitions, we were able to impact participants’ performance speed. Interestingly, while participants maintained the beneficial chunking pattern throughout the entire training period, participants that were able to abandon the detrimental pattern or combined more chunks could overcome the imposed performance detriment.

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Chapter 3

3 The role of feedback in the production of skilled finger sequences

3.1 Introduction

Most motor behaviours strongly depend on feedback. When we grasp a full cup and feel a sudden slip, we can swiftly adjust our grip force to avoid the cup slipping from our hand. This correction can occur in less than 100 ms (Cole and Abbs, 1988; Hernandez-Castillo et al., 2020; Johansson et al., 1992). Feedback from other senses such as vision (Day and Lyon, 2000; Veerman et al., 2008) and audition (Burnett et al., 1998; Howell, 2004) is also used for the control of an ongoing movements, albeit at slightly slower speeds (at 90-260 ms and 100-200 ms respectively). Based on the importance of sensory feedback, researchers have proposed that continuous feedback integration is essential for accurate movement execution (Adams 1971).

While much is known about the rapid sensory feedback integration during the execution of individual movements (for reviews see Cluff, Crevecoeur, & Scott, 2015; Scott, 2012; Shadmehr, Smith, & Krakauer, 2010), less is known about the integration of sensory feedback during the execution of sequences of finger movements. Previous studies investigating this topic have primarily focused on synchronization tasks in which participants are asked to synchronize their movements with an external variable such as a metronome or a musical piece (Aschersleben, 2002; Gates et al., 1974; Kulpa and Pfordresher, 2013; Pfordresher and Benitez, 2007; Repp, 2000; van der Steen et al., 2014). To probe feedback integration during the execution of fast finger sequences, feedback is commonly perturbed by delaying feedback presentation, either transiently or over a prolonged period of time. Using this approach, some studies

have reported an overall slowing of performance as a reaction to the perturbation (Gates et al., 1974; Kulpa and Pfordresher, 2013; van der Steen et al., 2014; Wing, 1977), whereas others observed a speed up in performance (Flach, 2005; Furuya and Soechting, 2010; Pfordresher and Palmer, 2002; Repp, 2000). This speed up has been attributed to an effort to maintain the imposed rhythm (Flach, 2005; Furuya and Soechting, 2010; Pfordresher and Palmer, 2002). Studies investigating non-constrained execution of rapid finger movements, however, are scarce (Jay and Hubbold, 2005; Long, 1975). Moreover, the majority of studies investigating this topic have focused on perturbing the slower visual or auditory feedback channels. Hence, these studies were unable to examine the full range of rapid feedback adjustments that are possible during a finger press.

Here we probed the use of sensory feedback during the execution of fast finger movement sequences. We manipulated haptic, visual, and auditory feedback on a few selected presses within a sequence, in a way that was not consciously perceivable by the vast majority of participants. Participants were trained on sequences of finger movements on an isometric keyboard throughout a four-day training period. On each press, upon reaching a given force threshold, participants were given a small haptic stimulus, similar to the feedback devices embedded in modern computer trackpads or smartphones. Concurrently, auditory and visual feedback indicated the successful pressing of the key. We then either delayed or advanced feedback on a single press within a sequence to probe how this sensory feedback is used in control. During the delayed feedback perturbation participants were not required to wait for the feedback to perform the subsequent presses – thus, by design, they could perform the task without considering feedback. However, we found an immediate, directionally-specific reaction to the feedback perturbation, providing strong evidence for the reliance of fast finger sequences on feedback.

The way participants react to a small feedback perturbation also provides a probe into how skilled motor sequences are organized. Models of sequence performance usually fall on a continuum along two extremes (Diedrichsen and

Kornysheva, 2015). On one side, sequences are controlled as a single unit or motor program (Keele, 1968) that specifies the detailed muscle commands necessary to produce the sequence (**Figure 3.1a**). On the other end is the idea that movement sequences are controlled hierarchically (Rosenbaum et al., 1983), in which one layer represents the sequence to be executed and another one generates the detailed muscle commands for each finger press (**Figure 3.1b**).

While both models would predict a modulation of the press that is perturbed, they differ in how subsequent presses would be affected. In the single motor program model, an acceleration or delay of a single movement element will shift the subsequent presses accordingly. In contrast, in the hierarchical model, the influence of a local sensory perturbation on a single finger could differ from the influence on subsequent presses. How exactly subsequent presses are influenced depends on how feedback is communicated from the lower-level finger controllers to the higher-level sequence controller (Kiebel et al., 2009), and how the sequence controller uses the feedback. By comparing the influence of a sensory feedback perturbation across finger movements of a sequence, we are able to gain novel insights into how sensory feedback is used in this organization.

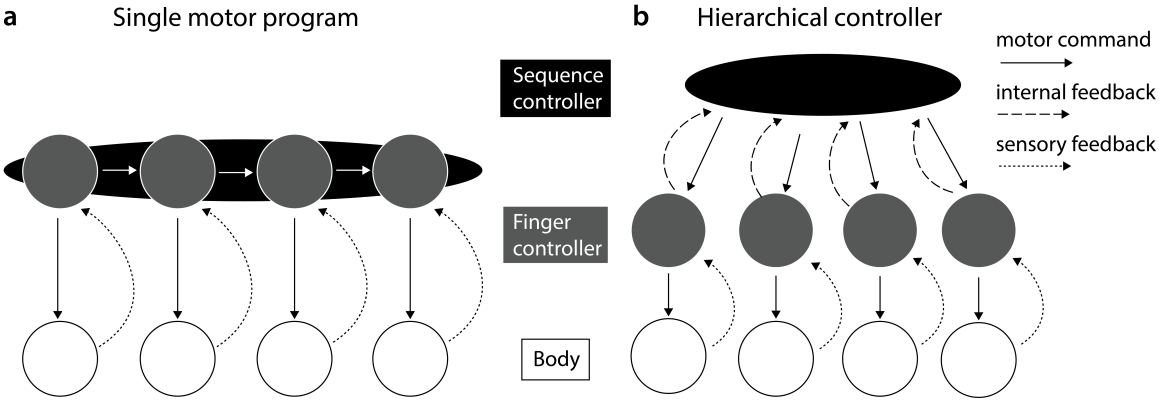


Figure 3.1. Two hypothetical representations of movement sequences. **(a)** A single motor program represents the movement sequence as an integrated unit. The completion of one finger controller automatically triggers the next finger controller. **(b)** A hierarchical controller represents the movement sequence across multiple layers that interact to produce the sequence of movements. The finger controllers represent the specific muscle commands for each of the fingers and are responsible for finger press execution. The sequence controller commands the finger controllers to initiate movements. In this particular model, the finger controllers provide internal feedback to the sequence controller when the finger press is completed. However, the next press may be initiated at a different time from the occurrence of the internal feedback

3.2 Methods

3.2.1 Participants

Twenty-six participants were recruited for this study (11 males; ages 18 to 44; mean age 25.5 [± 7.25]). All participants were right-handed (self-declared) and completed informed consent. On average participants had received 6.44 (± 7.25) years of musical training based on their longest played instrument, with 57% having at least one year of piano playing experience. The study protocol was approved by the ethics board of the University of Western Ontario and all participants gave their signed consent before starting the study.

3.2.2 Apparatus

To test participants, we used a custom-built five-finger keyboard (**Figure 3.2a**). The keys were not depressible but a force transducer (FSG-15N1A, Sensing and Control, Honeywell) was mounted underneath each key measuring isometric force production with a repeatability of <0.02 N and a dynamic range of 16 N (Wiestler et al., 2014; Wiestler and Diedrichsen, 2013; Yokoi et al., 2017). The digital sampling rate of the measured force was 200 Hz. Additionally, each key was equipped with a linear resonant actuator (LRA, LVM061930B-L20, Jinlong Machinery & Electronics Inc.) that provided haptic feedback during the experiment. LRAs vibrate at a frequency between 200 and 250 Hz. In our application, a haptic controller creates a specific waveform to elicit the click sensation. The haptic stimulation was produced by a haptic motor controller (DRV2605L, Adafruit Industries LLC) that produces a computer-controlled click/vibratory sensation that feels similar to the sensation experienced from smartphone keys or trackpads on laptops (see the DRV2605L dataset for more information regarding the specific waveform).

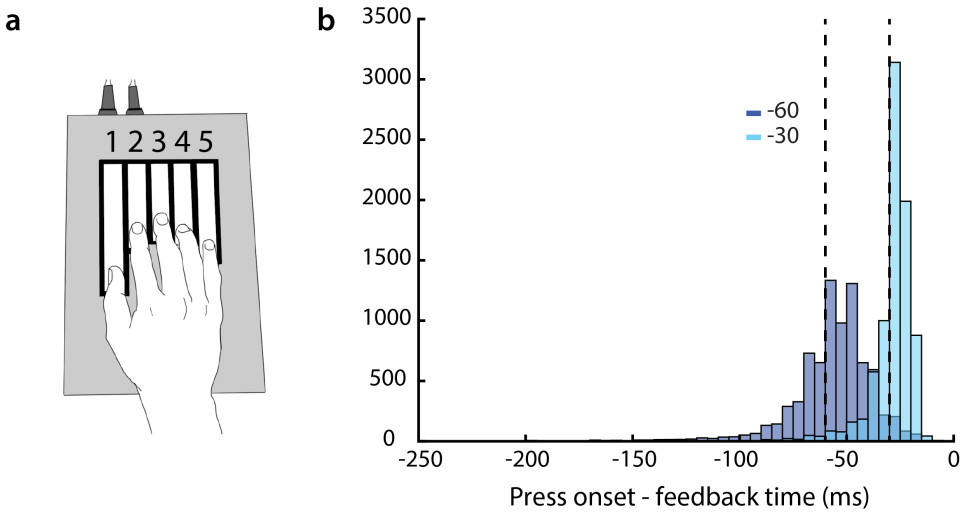


Figure 3.2 Apparatus and achieved time advancements of feedback. **(a)** Isometric keyboard-like device. Each key was associated with a number (these numbers were not shown to the participants but verbally explained). **(b)** Distribution of advancement times. Histogram of the time intervals between feedback presentation and press onset for the two advancement conditions. Vertical doted lines indicate -30 ms and -60 ms.

3.2.3 Discrete sequence production task

Participants performed a discrete sequence production task (DSP), executing sequences of 11 keypresses as fast and as accurately as possible. Participants were instructed to move as fast as possible, while maintaining an error rate of under 15% for each block of trials. Each finger was associated with a number (thumb = 1, index = 2, middle = 3, ring = 4 & little = 5). Each trial began with the presentation of a sequence of numbers on a computer screen (white font). A trial was deemed completed after 11 finger presses were executed. The numbers stayed on the screen throughout execution. Participants performed three sequences in total that were randomly presented to the participant. None of the sequences had directly repeating numbers (i.e., 33 or 44). The same three sequences were used for all participants; however, the presentation order was randomized across participants. Each block consisted of 39 trials and each sequence was presented 13 times during a block.

The force magnitude applied to each key by the participant was displayed as five lines on an LCD monitor, where each line height indicated the amount of force applied to the corresponding key. When the force on a key exceeded 1.5 N, the key press was registered and the feedback was triggered. Some co-articulation between fingers emerged as the next key could be pressed before the previous key was released.

When participants pressed the correct key, the visual cue on the screen turned green, a short pleasant auditory sound could be heard (each key was assigned a specific tone that was different from the rest) and a small click could be felt on the finger. We used the following notes for each key: thumb = A, index = C, middle = D, ring = E, little = G. If, however, an incorrect key was pressed, the visual cue changed to red, a lower-pitch sound could be heard (same across keys), and a click (same for accurate and incorrect press) could be felt.

For each completed trial participants received points based on their performance. If the participant pressed all keys correctly and their median

movement speed (MT - time between first press and last release) was within 95% to 110% of the current speed threshold (MT threshold) they received one point. If they correctly executed the sequence and their median movement speed was faster than 95% of the current MT threshold they received three points. If they pressed one or multiple keys incorrectly or their median speed was slower than 110% of their MT threshold they received zero points. At the end of a block, we provided participants with feedback regarding their error rate, median speed (MT), points obtained for the current block, and total points obtained across the session. To motivate participants to improve their performance throughout the sessions, we first set the MT threshold at 10 s at the beginning of each session and then adjusted it by lowering it to the median MT of a given block if the participant had a lower median MT compared to the current MT threshold and if their error rate was below 15%.

3.2.4 Feedback manipulation

The first three blocks in each session were completely unperturbed, meaning no feedback perturbation was presented. In each block afterwards, we perturbed 24 trials out of the 39 trials. On these perturbation trials, we either advanced or delayed the haptic, visual, and auditory feedback by 30 or 60 ms on one of the 11 key presses. To generalize our findings across fingers and press location within the sequence, we chose two fixed positions within each sequence where feedback perturbations were given. This also reduced the potential predictability of the perturbation location in each sequence. In sequence 1, we gave the feedback perturbation either at position 6 (finger 5) or 9 (finger 4), in sequence 2 at positions 4 (finger 2) or 7 (finger 1), and in sequence 3 at positions 5 (finger 4) or 8 (finger 3). In total, we presented the perturbation at six different sequence positions across all sequences.

For the advanced feedback conditions, we used an algorithm to predict when the feedback had to be given to occur either 30 or 60 ms before press

onset (the time at which the force on the key exceeded 1.5 N). This prediction was updated in real-time every 2 ms during trial execution. This prediction was based on three factors: the current force, the current force change (numerical derivative based on three time points) and the time since the last press onset. We separately trained this predictive model for each participant, sequence position and delay condition (-30 ms or -60 ms) using a logistic regression. This was done twice in each session. The first time we fit the model on the data from the first three blocks, using the unperturbed trials as training data. To account for speed changes during the session, we repeated the estimation in the middle of the session based on the unperturbed trials of all previous blocks (excluding the three initial blocks and at least six blocks of trials). The predicted outcome variable was zero if it was too early to present feedback and one if it was too late. Feedback was provided once the predicted probability exceeded 0.5. This approach led to an average time advancement of 29.3 ms (SD: 11.4 ms) for the -30 ms advancement condition and an average of 57.9 ms (SD: 23.3 ms) advancement for the -60 ms condition (see **Figure 3.2b**).

On the advanced trials participants could press the next key as soon as the feedback was presented on the current press, meaning they were allowed to press the next key before reaching the press threshold for the perturbed press. This led to an average of 2.36% (SD: 1.55%) of the advanced trials not reaching the press threshold. We excluded these trials from our analyses. Our analyses centered on calculating time intervals between specific press landmarks and the press onset of the perturbed press. In these trials the press onset was absent and thus we were unable to perform the same analyses.

In the delay conditions feedback was withheld upon reaching the press threshold, and instead presented 30 or 60 ms after press onset. However, in the delay conditions participants were not required to wait for the feedback to be presented before moving on to press the next press. This was important as participants did not have to take the feedback perturbation into account and

could potentially perform the sequences just as fast as when no perturbation was present.

3.2.5 Experimental Procedure

Participants completed four sessions that lasted approximately 1.5 hours each depending on how fast the participant was able to complete the required blocks of trials. Participants completed one session per day and the four sessions were scheduled over a timespan of approximately two weeks. Each participant completed a total of 74 blocks of trials across the four sessions. We encouraged participants to take breaks between blocks as necessary and offered a longer break in the middle of the experimental session. The participants were told that the goal was to perform the sequences as accurately and fast as possible. At the end of the four sessions we asked participants several questions about their experience that became more and more specific (see Appendix A). This questionnaire was used to determine whether participants were conscious of the experimental manipulation. Only two participants expressed clear conscious knowledge of the experimental manipulation, while the rest of the participants did not notice the manipulation. The performance of these two participants was similar to the performance of the other participants and therefore were not excluded from the analyses. Overall, the majority of participants were not consciously aware of our experimental manipulation, and hence we believe that they did not change their behaviour consciously.

3.2.6 Statistical Analysis

For each trial, we calculated the overall movement speed (movement time/MT) between the onset of the first press (first time it reached the press threshold) and the release of the last press (force fell below 1 N). Additionally, we found five landmarks (**Figure 3.3a**) for each press: early onset (*EO* - when force first was

great or equal to 0.75N), onset (*O* - when force first was equal or exceeded 1.5 N), peak (*P* - time at highest force – between onset and late release), release (*R* - when the force first fell under 1.5 N after peak), and late release (*LR* - when force first fell under 0.75 N after onset). All analyses were done relative to the onset of the perturbed press (or for unperturbed trials, the matching unperturbed press in the same sequence). We analyzed the relative timing of the landmarks on the perturbed press (+0), and the two presses after the perturbed press (+1 & +2).

All analyses were performed using custom-written code in MATLAB (The MathWorks) and the dataframe toolbox (github.com/jdiedrichsen/dataframe). We excluded any error trials from our analyses, as well as trials in which the press was delayed by more than 100 ms after the advanced feedback was given, as we believe that this could either suggest conscious awareness or an incorrect estimation from our algorithm that predicts when feedback should be given. We analyzed the data using paired one- and two-sample t-tests that were based on clear a priori predictions and we chose a probability threshold of $p<0.05$ for the rejection of the null hypothesis.

To estimate how quickly participants reacted to the delayed feedback by adjusting the perturbed press, we conducted a change point analysis. We first calculated the difference between the average force curves for the delayed trials (+30ms or +60ms) and unperturbed trials from 20 ms before press onset and 240 ms after onset. Using the data before the occurrence of the peak difference between the two curves, we estimated the time point when the difference started to emerge. We modelled the difference as a piece-wise linear function with a change point of b_0 between the two segments.

$$\hat{y}(t) = \begin{cases} 0\,, & t < b_0 \\ (t - b_0)b_1, & t \geq b_0 \end{cases}$$

where $\hat{y}(t)$ is the predicted force values for time t, b_0 is the chosen change point and b_1 is the slope of the function. Using the function fminsearch in MATLAB, we

found the values for b_0 and b_1 that minimized the sum of squares of the difference between observed and fitted data.

The single motor program hypothesis predicts that the perturbed press (+0) and the press following the perturbed press (+1) would be delayed or accelerated (relative to an average unperturbed press) by the same amount (**Figure 3.3b**). To test this idea, we examined the difference in the effect of the perturbation at a singular point in time across the consecutive presses (i.e. a point in time where the force curves of the presses overlap). We first chose a landmark at a time when the force curves of the two presses overlapped. At the end of training this overlap was clearly observed at the onset (1.5 N) of the +1 press for the unperturbed trials, which we chose as our reference landmark. On unperturbed trials we then found the average force for the +0 press, which defined our matching landmark (i.e. that occurred at the same point in time; see **Figure 3.3b**). We then calculated the effect of the perturbation on these two landmarks. The single motor program hypothesis predicts that both landmarks would be delayed by the same amount of time (relative to an unperturbed press). In contrast, a difference in delay (positive or negative) between the +1 press and the +0 press would indicate that the effect of the perturbed feedback was not the same for the two presses.

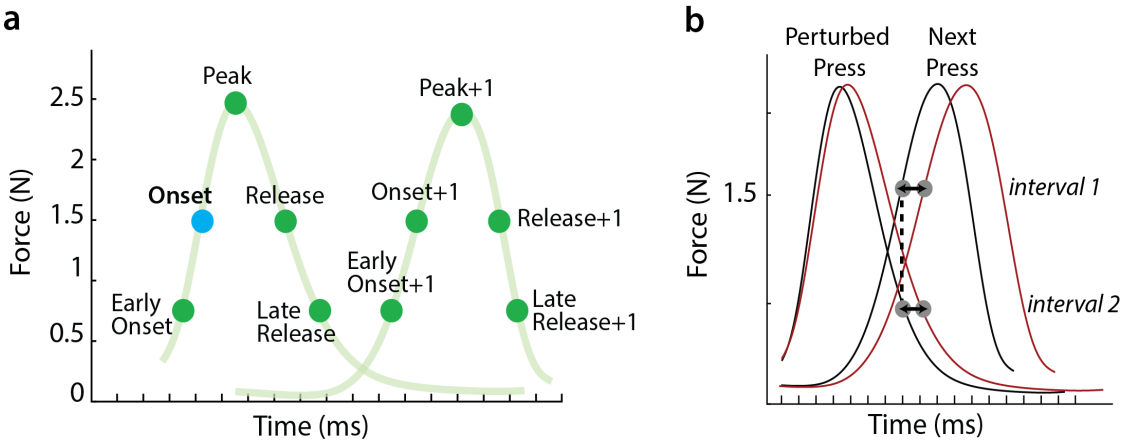


Figure 3.3. **Calculation of feedback differences across presses and landmarks.**

(a) For our analyses we calculated time intervals between the onset of the perturbed press (blue onset dot in the figure) and different force landmarks (green dots) on the perturbed press as well as on subsequent presses (indicated with +1). We chose five specific force landmarks on each press: Early Onset (>=0.75 N), Onset (>=1.5 N), Peak (maximum N between onset and release of press), Release (first time <1.5 N after onset), and Late Release (first time <0.75 after onset). **(b)** We choose a single time point (onset of next press) and compared how the perturbation affected this time point across presses. The black line indicates unperturbed trials and red lines represent perturbed trials.

3.2.7 Control experiment

In a separate experiment we probed to what degree the modality of the sensory feedback (auditory, haptic and visual) had differential effects on participants' performance. We recruited 48 participants for this experiment. They were assigned to one of the three feedback groups (auditory, haptic or visual) at the beginning of training based on an algorithm that matched participants' speed, calculated as the time between the onset of the first press to the release of the last press (MT). This was done to ensure that the groups had similar average speeds at the start of the experiment. Participants only received one type of feedback throughout the study (how each feedback was given was the same as described in the experimental design above). When an incorrect finger press occurred, all groups saw the visual cue on the screen turn red to make it easier for them to know where they made the error in the sequence. Participants practiced four different sequences (three were the same as in the main experiment) for five days on the same keyboard-like device. Press threshold was 1 N. Because of the difference in press threshold we adjusted our landmark criteria for this experiment: early onset (*EO* - when force first was great or equal to 0.6 N), onset (*O* - when force first was equal or exceeded 1 N), peak (*P* - time at highest force – between onset and late release), release (*R* - when the force first fell under 1 N after peak), and late release (*LR* - when force first fell under 0.6 N after onset). Feedback perturbations were given on a single press within the sequence at two possible locations (similar to the main experiment but the locations were not identical). In this experiment we only perturbed participants' feedback by delaying it by 80 ms. The rest of the experimental design was identical to the main experiment (point system, threshold change, etc.). As in the main experiment, most participants were unaware of the perturbation when asked about it using a questionnaire at the end of the sessions.

3.3 Results

3.3.1 Feedback perturbations cause directionally specific behavioural adjustments to the perturbed finger press.

To investigate how sensory feedback is used during the execution of fast finger sequences, we used transient perturbations of the sensory feedback that indicated the successful pressing of a key. The perturbation was only applied to a single press within a sequence. Participants practiced three different sequences over four days. If sensory feedback is used to control the near-isometric keypress, the delay and advancements of feedback should prolong or shorten the ongoing press, respectively.

The group average force traces (**Figure 3.4a**) indicated that even though each finger press was completed within ~300 ms, participants indeed reacted to the feedback perturbation by extending or shortening the ongoing press. To quantify this effect, we calculated the time interval between the onset (first time >=1.5 N is reached) and the peak (onset-peak) of the perturbed press (**Figure 3.4b** onset-peak), as well as the interval between the onset and the release (first time <1.5 N after onset; **Figure 3.4b** onset-release). On day 1, both the +30 ms ($t_{(25)}$ = 11.189, p= 1.59e-11) and the +60 ms delay condition ($t_{(25)}$ =4.969, p= 2.02e-05) resulted in a longer onset-peak interval. Similar effects can also be seen on the interval between onset and release (+*30 ms*: $t_{(25)}$ = 6.630, p = 3.01e-07, +*60 ms*: $t_{(25)}$ = 5.963, p = 1.58e-06). For the time advanced feedback conditions, the onset-release intervals on day 1 were shortened in response to perturbations (onset-release -*30 ms*: $t_{(25)}$ = 5.308, p = 8.42e-06; -*60 ms*: $t_{(25)}$ = 4.291, p = 3.78e-10). These results suggest participants used sensory feedback to finely control the duration of the force production.

3.3.2 Perturbation effects diminish but do not disappear with training

Does feedback control still play a role in movement execution at the end of training? If the motor system uses sensory feedback to control the execution of extensively practiced finger movements, we expect the feedback perturbation to still impact the duration of the press at the end of training. Indeed, this was what we found (**Figure 3.4a** vs. **3.4c**). Specifically, both delay conditions showed longer onset-peak intervals (+*30 ms*: $t_{(25)}$ = 5.963, p = 1.17e-04; +*60 ms*: $t_{(25)}$ =6.420, p= 5.05e-07) and onset-release intervals (+*30 ms*: $t_{(25)}$ = 6.143, p = 1.01e-06, +*60* ms: $t_{(25)}$ = 5.082, p = 1.51e-05) compared to the unperturbed condition on day 4 of training (**Figure 3.4d**). Similarly, shorter onset-release intervals were observed for the advancement conditions (day 4 onset-release *-30 ms*: $t_{(25)}$ = 3.774, p = 4.46e-04, *-60 ms*: $t_{(25)}$ = 4.785, p= 3.26e-05). The finding of a clear adjustment of the perturbed press at the end training suggests that even skilled performance is controlled by sensory feedback.

While the overall effect was clearly present across all days, the effect caused by the large perturbations reduced by ~40%. Specifically, the difference between perturbed and unperturbed onset-release interval reduced from day 1 to day 4 for the +60 ms (-38%, $t_{(25)}$ = 2.502, p = 0.019) and the -60 ms condition (-40%; $t_{(25)}$ = -3.859, p = 7.106e-04). While the overall effect also reduced for the smaller perturbations, these changes were not significant (+30 ms: -29%, $t_{(25)}$ = 1.848, p = 0.076; -30 ms: -35%, $t_{(25)}$ = -1.639, p = 0.113). This suggests that some transition from feedback to feed-forward control took place in our task with practice.

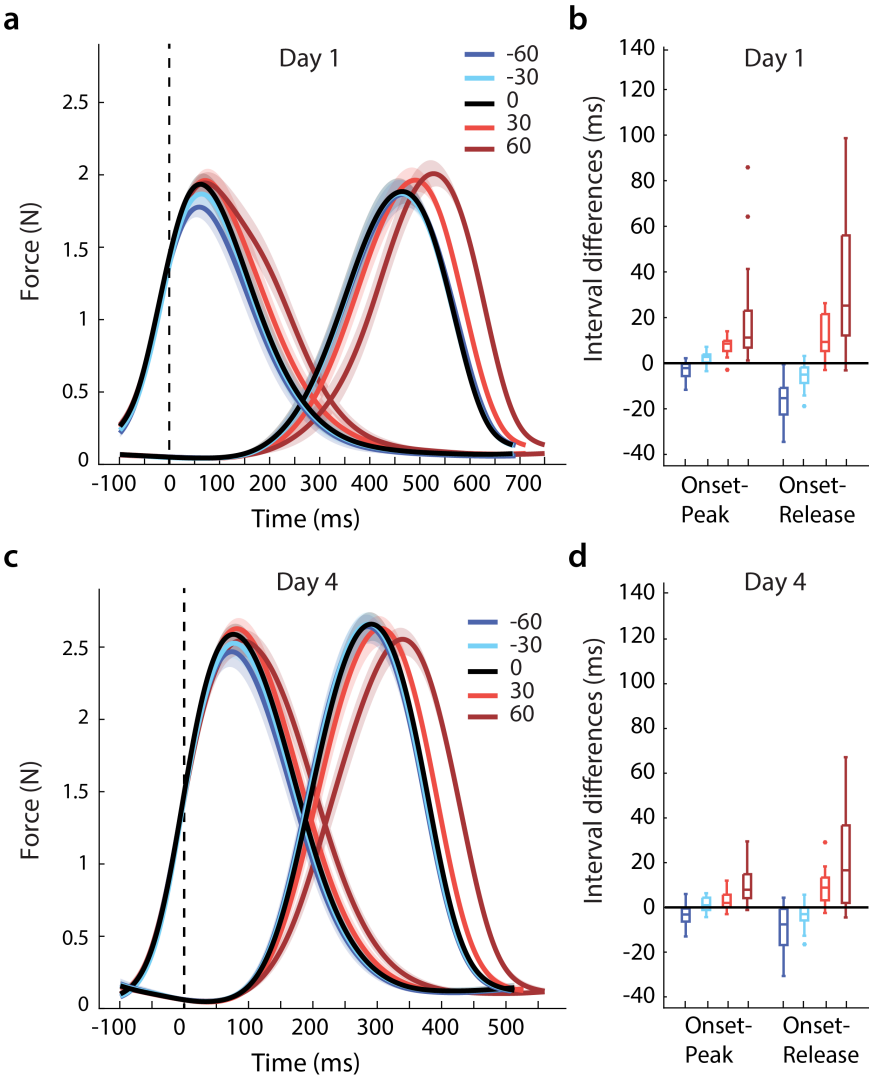


Figure 3.4. Effects of perturbation on perturbed press and subsequent press.

(a) & **(b)** Average force traces for day 1 and 4 and the following press interpolated and standardized to the average time of each condition. Dotted line indicates press onset, for which the sensory feedback was shifted in time. Error bars represent the standard error of the mean across participants. **(c)** & **(d)** Differences between the onset-to-peak and onset-to-release intervals of perturbed and unperturbed trials for day 1 and day 4.

3.3.3 Perturbations lead to reactions within 80ms

How quickly is sensory feedback taken into account to control the ongoing finger press? To estimate this, we first calculated a difference curve between the average force traces of the delayed perturbation conditions and the unperturbed condition for each participant. We then used a change point analyses (see methods for details) to estimate the time at which the difference curve was impacted by the feedback delay. On day 1 in the +60 ms delay condition, it took an average of 106.4 ms (95% CI [97.77, 115.03]) after press onset for participants to show a divergence between the two force traces. For the +30 ms delay condition we saw a difference at 77.3 ms (95% CI [64.65, 90.04]) after press onset. For day 4, our estimate of adjustment onset for the +60 ms condition was 92.5 ms (95% CI [83.04, 101.97]), faster than day 1 ($t_{(25)} = 2.085$, $p = 0.047$). The estimate for the +30 ms condition was comparable to day 1 (mean: 67.5; 95% CI [46.32, 88.72]; $t_{(25)} = 0.738$, $p = 0.467$). Thus, the adjustment of the ongoing press to the delayed feedback was consistently very fast.

3.3.4 Subsequent presses are delayed irrespective of perturbation direction

So far, we have established that sensory feedback about the keypress is used to control the finger that produces the press, even during fast performance after extended training. Next, we investigated how the subsequent presses are impacted by the perturbation. This provides us with an opportunity to compare different models of how skilled movement sequences are organized.

To visualize how the perturbations influenced both the current and subsequent presses, we plotted the timing of five events (early onset, onset, peak, release, late release, see Methods) for the perturbed and the two subsequent presses across the four sessions (**Figure 3.5**). As the independent variable (i.e. x-axis) we plotted the group-averaged time estimates of these landmarks for the non-perturbed trials relative to the onset of the perturbed press

(0 ms). As the dependent variable (i.e. y-axis) we plotted the change in the average time interval relative to the unperturbed condition. Each press is indicated by a line that connects the five corresponding landmarks.

The feedback perturbations impacted not only the execution of the current press, but also of subsequent presses. On the first day of training, both the +30 ms perturbation ($t_{(25)}$ = 6.055, p= 2.51e-06) and the +60 ms perturbation ($t_{(25)}$ =9.078, p= 2.177e-09) delayed the onset (interval onset-onset+1) of the next press relative to when no perturbation was present (i.e. red lines vs. grey line at zero). Moreover, the delay of feedback impacted even the onset of the press two positions after the perturbation (+*60 ms*: $t_{(25)}$ = 7.172, p= 8.11e-08). In contrast, time advancements did not alter the timing of subsequent presses relative to the unperturbed trials (onset-onset+1: -*30 ms*: $t_{(25)}$ = -0.904; p = 0.375; -*60 ms*: $t_{(25)}$ = -1.488, p = 0.149). This pattern of results provides new insights into how feedback is used in the control and representation of skilled movement sequences (as outlined in the introduction, **Figure 3.1**).

If trained sequences are encoded as a single motor program (**Figure 3.1a**), the control of one finger directly influences the control of the subsequent finger. This prediction becomes directly testable when there is considerable overlap, i.e., coarticulation, across different finger presses. Such coarticulation was observed on days 3 and 4 (**Figure 3.5**; where the onset of the second press roughly occurred at the same time as the release of the perturbed press). For such overlapping presses, the single motor program hypothesis would predict that the relationship between the release of the perturbed press and the onset of the next press in the sequence will be the same, even if the entire motor program is sped up or slowed down. In other words, the effect of the perturbation should be the same for simultaneous events on two overlapping presses. To test this idea, we used the data from the last day of training. We compared the effect of the perturbation on the onset of the next press (onest+1 **Figure 3.5**) with its effect on the perturbed press at the same point in time (see Methods for detail). We found a significantly longer delay for the subsequent press in comparison to

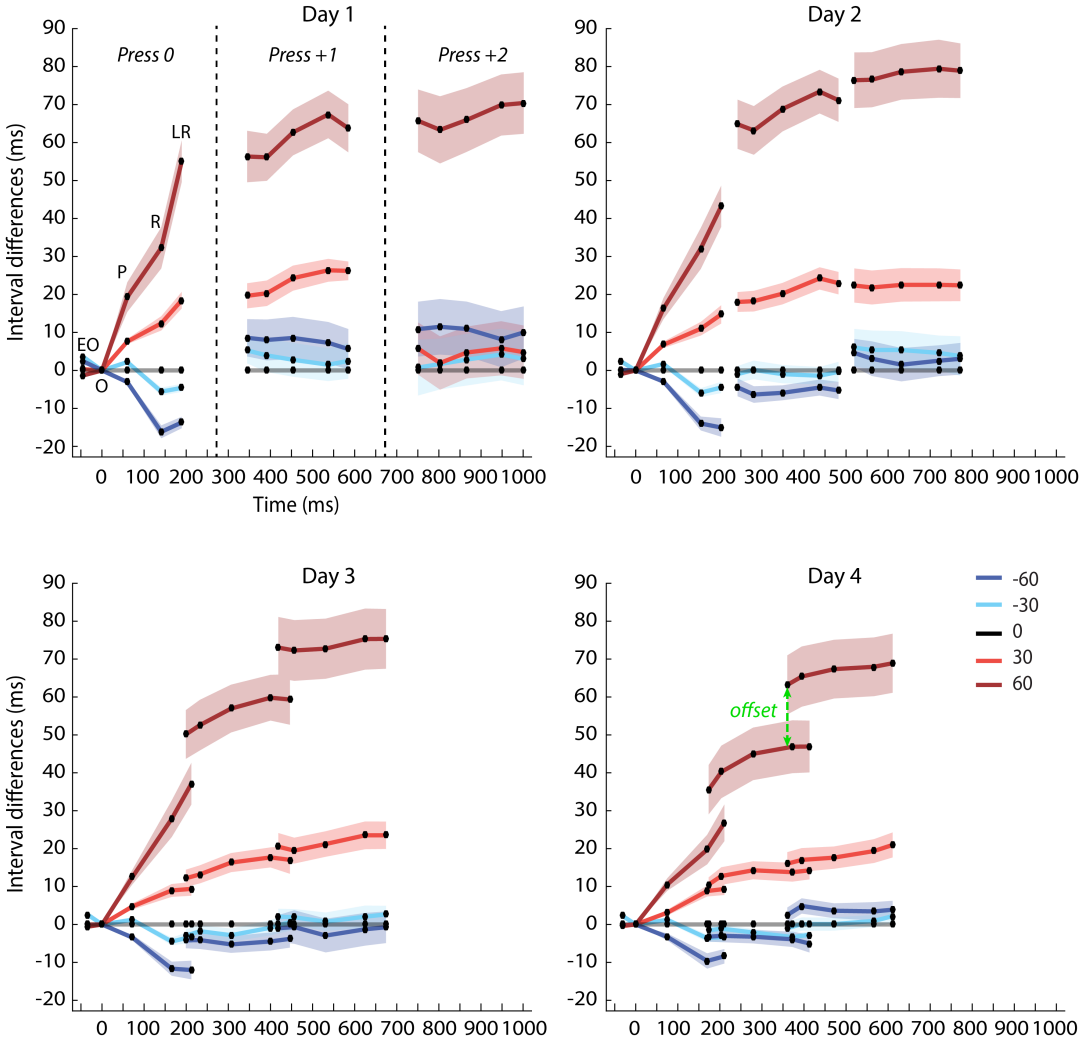
the perturbed press for the +60 condition ($t_{(25)}$ = 2.522, p = 0.018). This effect can be seen as an offset between the end of the line for the perturbed press and the onset of the line of the subsequent press in **Figure 3.5** (day 4). A similar offset between presses was also present between the second and third press after the perturbation ($t_{(25)}$ = 3.429, p = 0.002). These additional delays across presses resulted in an overall slower execution speed for the entire sequence (MT; day 4: *+60 ms*: $t_{(25)}$ = 5.828, p = 4.456e-06). These findings provide clear evidence against the idea that the sequence is represented as a single motor program after training. Rather it argues for a hierarchical organization (**Figure 3.1b**), in which the effects on the subsequent finger presses can differ from the effect on the perturbed finger.

The participants' reactions to the other perturbation conditions provide us with more detailed insight into how feedback is considered in this hierarchical organization. Similarly to what we have observed for the +60 ms delay condition, an offset between the different presses was also observed for time-advancement of the feedback by -60 ms (dark blue in **Figure 3.5**), although this effect did not reach significance ($t_{(25)}$ = 2.043, p = 0.052). Nevertheless, the offset was significant when comparing the second and third press after the perturbation ($t_{(25)}$ = 3.877, p = 6.799e-04). In the -60 ms perturbation condition, these additional offsets did not result in a significant slowdown of the overall sequence speed (Day 4: $t_{(25)}$ = -0.858, p = 0.399), suggesting that the additional delays of subsequent presses were cancelled out by the speed-up on the perturbed press. In contrast to the ±60 ms feedback perturbations, no clear offset was present for the ±30ms perturbation condition (**Figure 3.5** – light blue and light red). Indeed, the comparison did not reach statistical significance for either time delay (*+30 ms*: $t_{(25)}$ = 0.882, p = 0.193) or advancement perturbation (*-30 ms:* $t_{(25)}$ = 0.589, p = 0.281). In sum, for larger but not for smaller perturbations participants delayed subsequent presses after the occurrence of a perturbation, irrespective of whether the sensory feedback was advanced or delayed.

Overall, our findings suggest a hierarchical organization in which sensory feedback acts in two qualitatively different ways. First, the timing of the feedback *directionally* either lengthens or shortens the perturbed key press. Second, the occurrence of a perturbation also appears to act in a *directionally non-specific* manner slowing down the execution of future presses. This effect was stronger for larger (60 ms) compared to smaller (30 ms) perturbations but did not depend on the direction of the temporal shift.

Figure 3.5. Effects of feedback perturbation on the perturbed press (press 0) and subsequent finger presses (Press +1, +2) across feedback conditions and training days.

Five landmarks (EO: early onset, O: onset, P: peak, R: release, LR: later release) are plotted per press (see methods). The x-axis shows the average time of occurrence of the landmark on unperturbed trials relative to the onset of the first press. The y-axis shows the time interval differences between the perturbation conditions and the unperturbed condition on the particular landmarks. Landmarks belonging to a finger press are connected by a line. Anything above the 0 line indicates that the perturbation resulted in longer time intervals (i.e. slower) compared to when no perturbation was present, whereas everything below the line indicates shorter time intervals (i.e. speed-up). The different panels indicate the different training sessions (i.e. days). Day 4 shows how we tested the offset between presses, with an example of the 2nd to 3rd press for the +60ms condition. Error bars represent the standard error of the mean across participants.


Day 1
Day 2
Day 3
Day 4
Press 0
Press +1
Press +2
LR
R
P
EO
O
offset
-60
-30
0
30
60
Interval differences (ms)
Time (ms)

3.3.5 Rapid behavioural adjustments are caused by haptic feedback

Finally, we investigated to what degree the effects observed in the main experiment were due to the perturbation of haptic, visual, or auditory feedback. To test this, we conducted a control experiment, in which a separate set of participants was assigned to one of three experimental groups, with each group receiving only one of the three types of feedback (auditory, visual or haptic). As in the main experiment, we delayed the feedback on selected finger presses within the sequence. In this case, we only chose a single perturbation condition (delay +80 ms) and participants practiced the task for five days. Examining the effect of the delay on the perturbed press (see **Figure 3.6**), we found that only the haptic group demonstrated a significantly longer onset-peak interval following the perturbation both in the beginning (Day 1: $t_{(15)} = 2.980$, $p = 0.009$) and towards the end of training (Day 4: $t_{(15)} = 3.579$, $p = 0.003$). Neither the visual (Day 4: $t_{(15)} = 0.901$, $p = 0.382$) nor the auditory group (Day 4: $t_{(15)} = 1.060$, $p = 0.306$) showed a significant effect of the feedback perturbation on the onset-peak interval. These results clearly show that the rapid adjustments of the ongoing press were driven by haptic feedback from the fingertip.

3.3.6 Delay of subsequent presses arises from all three feedback modalities

In contrast, the delay of subsequent presses was observed for all three feedback modality groups. Consistent with the effect on the perturbed press, the delay of the onset of the press following the perturbation (+1, averaged across days 2-5) was largest in the haptic group (69 ms, $t_{(15)} = 6.890$, $p = 5.146e\text{-}06$). However, both the auditory group (35 ms, $t_{(15)} = 4.888$, $p = 1.971e\text{-}04$), as well as the visual group (19 ms, $t_{(15)} = 4.828$, $p = 2.214e\text{-}04$), showed a clear delay in the onset of the subsequent press, even though no such effect was observed on the perturbed press (**Figure 3.6**). This result suggests that the delay we observed on

the subsequent presses in our main experiment could be induced by the perturbations in each of the three feedback modalities.

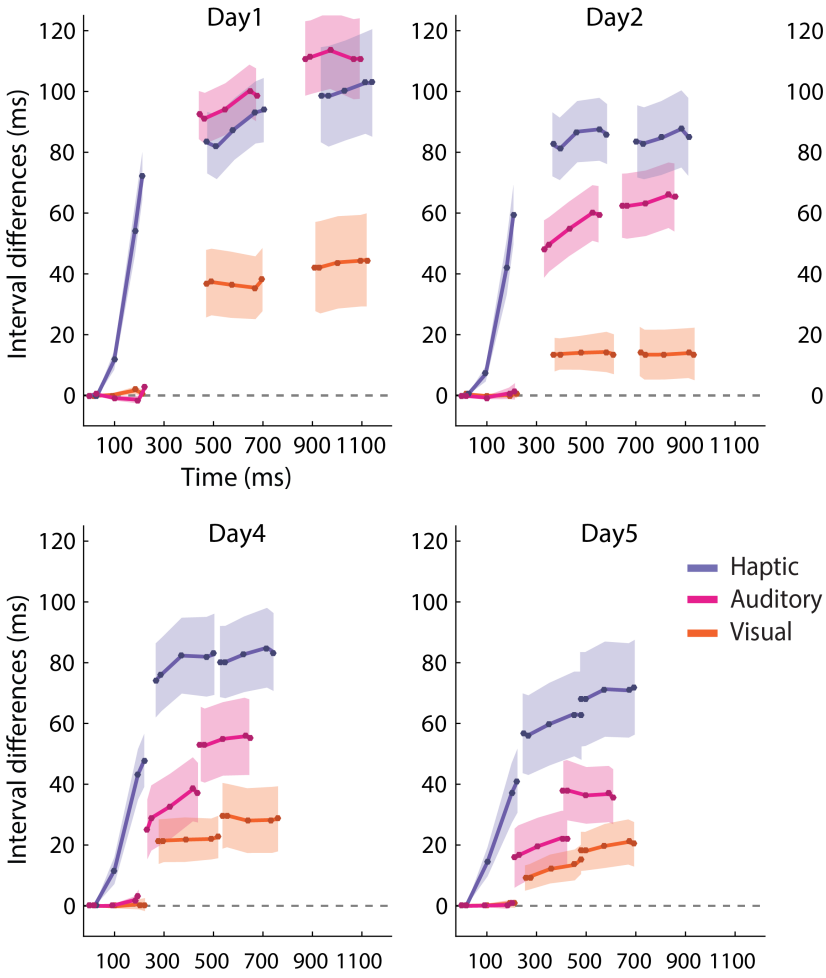


Figure 3.6. Effect of feedback perturbation for haptic, visual and auditory groups in control experiment across training days.

As in **Figure 3.5**, five landmarks per press (connected by a line) are plotted. The control experiment only had +80ms perturbations, but each group received only one type of feedback. The different panels indicate the different training sessions (i.e. days). The error bars represent the standard error of the mean across participants for each group.

3.4 Discussion

In this study, we used small transient feedback perturbations to probe how sensory feedback is used in the control of fast finger movement sequences. Specifically, we examined how sensory feedback modulates the execution of skilled finger movements across four days of training, and how feedback differentially affects the execution of the ongoing press and subsequent presses.

3.4.1 Sensory feedback modulates movement execution throughout skill acquisition

Throughout training, we found clear evidence of rapid behavioural adjustments on the finger press that received the perturbation. This result illustrates the continuous integration of sensory feedback when controlling skilled finger movements. Participants adjusted their ongoing behaviour even though our task was designed so that it could be accomplished without considering the feedback. The keypresses were isometric and participants simply needed to exceed a specific force threshold. In the delay condition, we decoupled sensory feedback and force threshold by delaying the feedback. In this case, participants needed to exceed the force threshold but they did not need to wait for the feedback to produce the next press. Nonetheless, participants adjusted their behaviour based on the perturbation.

Furthermore, we found that the effects of the perturbation were directionally specific: The delay in sensory feedback resulted in a lengthening of the perturbed press, whereas a time advancement resulted in a shortening. Previous studies have primarily investigated feedback delays (Furuya and Soechting, 2010; Howell and Archer, 1984; Sakata and Brainard, 2006; van der Steen et al., 2014) but have rarely advanced participants' feedback (Repp, 2002; Wing, 1977). By including both feedback delays and advancements we provided evidence of the directional nature of sensory feedback integration in fast non-constraint finger movements.

The reaction to the delay of haptic feedback was very fast and occurred within 60-90 ms after the expected time of the feedback. This finding is consistent with previous reports that demonstrate responses between 65-110 ms following a haptic input (Abbs et al., 1984; Pruszynski et al., 2016; Scott, 2016). In contrast, auditory and visual feedback alone did not elicit a strong reaction on the press, consistent with the fact that the quickest reactions to changes in these two modalities are noticeably slower (Burnett et al., 1998; Day and Lyon, 2000; Howell, 2004; MacKenzie and Marteniuk, 1985; Smith and Bowen, 1980; Veerman et al., 2008). Therefore, by including a haptic feedback condition we were able to show the very rapid integration of sensory feedback in the execution of a finger press.

3.4.2 Shift from feedback to feed-forward control with learning

While the feedback perturbation still significantly impacted the execution of the perturbed press on the last day of practice, we did find that the effect reduced by approximately 40% with training. This observation is in line with previous research that observed a shift from feedback to feed-forward control with training (Pew, 1966; Seidler-Dobrin and Stelmach, 1998). It has been suggested that feedback plays an important role in the initial phases of acquiring a novel motor skill, but its importance decreases, and potentially even disappears altogether, with prolonged training (Pew, 1966; Pratt et al., 1994; Schmidt, 1975; Schmidt and McCabe, 1976; Seidler-Dobrin and Stelmach, 1998). One theoretical consideration behind this idea is that, as we acquire an accurate internal representation of the instructed movements, sensory feedback becomes less necessary for execution (MacNeilage and MacNeilage, 1973; Schmidt, 1975; Seidler-Dobrin and Stelmach, 1998). However, it is unclear whether the decrease in perturbation effects we observed was indeed driven by a change in internal model accuracy. Another possible explanation is that participants learned that the feedback was not directly related to their performance (Wei and Körding, 2009) and that they could therefore perform the task accurately and fast without taking

the feedback into consideration. If this was the case, however, it is unclear why we only saw a reduction in the larger perturbations but not in the smaller ones.

3.4.3 Hierarchical organization of feedback control in sequential movements

Our second main goal was to understand how sensory feedback is being taken into account in the control of a complex motor sequence. Models of sequence representation fall between two opposing extremes: A single, integrated motor program, and a strict hierarchical organization (**Figure 3.1**). By examining how feedback is integrated across multiple finger presses, we were able to get a better grasp of this underlying organizational structure and how feedback is integrated across the different layers.

We found that the feedback perturbation on a single press also affected the execution of subsequent presses, both at the beginning and at the end of training. Important, the reaction to the feedback perturbation was different for the perturbed and subsequent presses. This finding argues against the idea that after prolonged training a movement sequence is represented as a single motor program (Keele, 1968), in which each finger is affected in the same way by the perturbation. Instead, our results more closely align with the idea of a hierarchical organization (Rosenbaum et al., 1983), in which the sequence is controlled through the interaction of different layers that control sequence execution. One possible organization is a two-tiered structure (**Figure 3.1b**), in which a sequence controller is positioned at the highest level representing the specific order of movements and commanding the next layer of finger controllers, which in turn are responsible for the control of specific finger movements. Our results suggest three important processes in how this system deals with sensory feedback:

First, we found that the sensory feedback from the finger itself is continuously relayed to the finger controller which then impacts the ongoing movement execution in a directional specific manner. Second, upon receiving the

sensory feedback signifying press completion, the finger controller issues a completion signal to the sequence controller. Our finding that feedback not only impacts the ongoing press but also subsequent presses, demonstrates that information is relayed across all hierarchical levels. Third, we found that both feedback advancements and delays led to an overall slower initiation of the next finger in the sequence. One possible mechanism is that the sequence controller compares a prediction of when a completion signal is expected vs. when it is received and, upon mismatch, delays the execution of the next press as a cautionary measure. We also found that only the two larger sensory feedback perturbations led to a significant delay, suggesting that the cautionary response is proportional to the amount mismatch between expected and received feedback from the lower-level controller. Additionally, the sequence controller also showed a reaction to a delay or time advancement in auditory and visual feedback, which did not influence the local press, indicating that the sequence controller also has direct access to sensory feedback signalling whether the goal of an action has been achieved.

Previous research studying time delays and advancements of an external pacing signal in a synchronization paradigm (Furuya and Soechting, 2010; Repp, 2000; Wing, 1977) also show evidence for feedback adjustments in a hierarchical sequence controller. In contrast to our experiment, in which a feedback perturbation led to a delay irrespective of direction of the perturbation, these adjustments were targeted to bring the finger tapping back into synchronization with the metronome (Furuya and Soechting, 2010; Repp, 2000). In our paradigm, participants' speed was not constrained by any external variable (such as a metronome), so performance was not directed to preserve a rhythm. Together these results suggest that the reaction of the sequence controller to feedback perturbation strongly depends on the task goal.

3.4.4 Conclusion

In this study, we demonstrated that sensory feedback is continuously used to adjust movement execution but that the extent of this integration diminishes with training. Haptic feedback drove the effects we observed on the perturbed press, whereas the effects across the remaining movements in the sequence were impacted by the perturbation in all three feedback modalities. Lastly, we demonstrated distinct types of feedback processes involved in the hierarchical control of skilled finger sequences.

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Chapter 4

4 General Discussion

4.1 Overview

The overarching aim of this thesis was to advance our understanding of the control and representation of finger movement sequences. These topics were investigated using a discrete sequence production task in which participants had to perform sequences of isometric finger movements as fast and accurately as possible. More specifically, in **chapter 2** we investigated the relationship between the mental representation of a sequence and its performance. We were able to shape participants' initial mental representation to be either beneficial or detrimental to performance and observed how these initial instructions impacted performance long-term. In **chapter 3,** we used sensory feedback perturbations to test how sensory feedback is integrated during movement execution and whether this integration changes with training. The following discussion is divided into four sections. The first part will focus on our findings related to the hierarchical representation of finger movement sequences and how the structure of such representations pertains to performance. Section two will outline arguments about the mechanistic underpinnings of the natural formation of hierarchical representations. In the third part, I will review our results regarding the use of sensory feedback during sequence execution and expand on the possible mechanisms that could underlie the training-related changes we observed. Part four is an opinion section, in which I discuss the relationship between task diversity and result generalization.

4.2 Hierarchical organization of skilled movement sequences

One of the key findings we observed across both projects is that sequences of skilled finger movements are hierarchically organized (**Figure 4.1**). In **chapter 2**, we demonstrated that participants concatenated chunks with training, but did not merge the sequence into a single chunk even after extensive training. Instead, participants on average still subdivided the sequence into three chunks. We believe that in combination with our finding that participants' chunk structure crystalized with training, this provides a strong argument for the hierarchical representation of skilled movement sequences.

In **chapter 3**, we found that the feedback perturbation had distinct effects on finger press execution at the end of training. Specifically, we observed that the press following the perturbation was impacted to a greater degree than the perturbed press. The observed difference could only occur if the finger controllers are governed by a higher-level controller (i.e., sequence controller). This higher-level controller can modulate ongoing movement execution by adjusting the finger controllers independently (**Figure 4.1**). Therefore, this finding provides further evidence for a hierarchical organization of skilled finger movement sequences and opposes the idea that with training, sequences become organized as a single motor program (Rozanov et al., 2010). In summary, using two different approaches to study the representation of skilled finger movement sequences, we demonstrated the importance of hierarchical organization for skilled sequential actions.

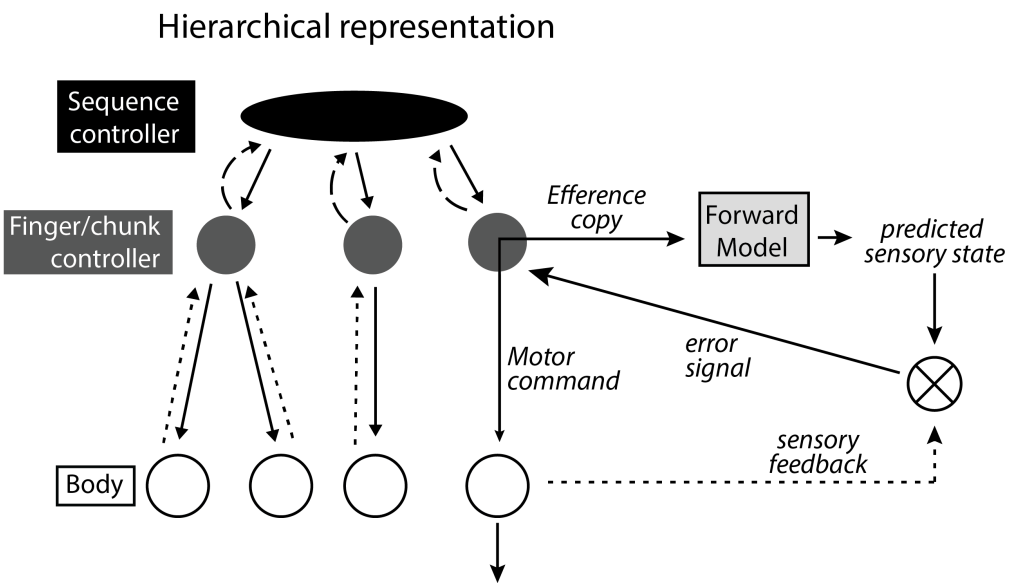


Figure 4.1. Hierarchical organization of sequence representation with feedback mechanism.

Abstract hierarchical representation of a movement sequence with three levels. It includes a representation of how feedback is integrated and shapes the motor command. The finger controller submits a motor command to the body to produce movement. Sensory feedback is then compared to a predicted state and any discrepancy results in an error signal that then adjusts the ongoing motor command.

4.2.1 Neuronal underpinnings of a hierarchical sequence representation

The neuronal underpinnings of such a hierarchical system have yet to be fully formalized. However, several propositions have been advanced regarding the brain regions involved at different levels of the hierarchy. The primary motor cortex (M1), the cerebellum, and the primary somatosensory cortex (S1) have been considered prime candidates for the lower levels of the hierarchy. Brain regions at these levels are theorized to be responsible for the execution of motor primitives and the integration of sensory feedback. As described in **chapter 1**, M1 is involved in the execution of single finger presses but does not appear to be encoding sequence-specific characteristics (Berlot et al., 2020; Yokoi et al., 2018; Yokoi and Diedrichsen, 2019). The cerebellum plays a critical role in the generation of predictive models (Parrell et al., 2017; Shidara et al., 1993) and is suggested to be an important region for the acquisition and transformation of internal models (Kawato, 1999; Wolpert and Kawato, 1998). Hence, together with S1, this region appears to be crucial for the integration of sensory feedback during movement execution. The shift from feedback to feed-forward control we observed in **chapter 3,** could indicate an increased involvement of the cerebellum as learning progresses (Izawa et al., 2012; Pisotta and Molinari, 2014).

The basal ganglia potentially play a role in the connection between the lower and higher levels of the sequence hierarchy. The striatum, in particular, is involved in the temporal segmentation (chunking) of sequences (Geddes et al., 2018; Jin et al., 2014; Jin and Costa, 2015; Levesque et al., 2007; Markowitz et al., 2018), and in the exhibition and encoding of motor habits (Graybiel, 2008; Tricomi et al., 2009; Yin and Knowlton, 2006). In line with this idea, Tremblay and colleagues (2010) observed that movement segmentation is dopamine-dependent. They found that movement chunking is absent in Parkinson's patients (Benecke et al., 1987) but can be restored with levodopa treatment (Tremblay et al., 2010). In sum, the basal ganglia could be important for the

interplay between the lower and higher levels of the hierarchy by being responsible for movement segmentation early in training (Miyachi et al., 1997) and habituation later in training.

Higher-order association regions have been proposed to reside at the highest level of the hierarchy. Neural activity in the supplementary motor area (SMA) is sensitive to the sequential order of upcoming movements. This potentially implies a role of SMA in the temporal order of sequence execution (Tanji and Shima, 1994). With the anatomical connection from the basal ganglia to SMA via the thalamus (Akkal et al., 2007; Sakai et al., 1999), it is conceivable that the sequence segmentation is forwarded from the basal ganglia to SMA, which in turn is responsible for the temporal order of the movement chunks. Additionally, SMA is said to be responsible for the aggregation of the distinct movement elements into a united motor plan (Gentilucci et al., 2000), which could be driven by input from the cerebellum (Akkal et al., 2007). Pre-SMA and SMA have been suggested to play different roles during sequence learning (Kennerley et al., 2004; Nakamura et al., 1998). Activity in pre-SMA is greater early in training and reduces as training continuous (Hikosaka et al., 1996; Sakai et al., 1998). This could suggest its involvement in chunk formation, which occurs early on in training. Additionally, pre-SMA is also active when a movement plan has to be changed (Matsuzaka and Tanji, 1996). In contrast, SMA seems to be more active for learned sequences (Hikosaka et al., 1996). Given this information, we would predict a dissociation between Pre-SMA and SMA activity in **chapter 2** across training. We would predict greater pre-SMA activity for the disadvantageously instructed sequences compared to the advantageously instructed ones, as participants changed their chunk pattern more readily for the former. In contrast, more SMA activity could be expected for the beneficially instructed sequences throughout practice.

Besides SMA, the prefrontal cortex has also been implicated in sequence learning (Badre and Nee, 2018; Mushiake et al., 2006; Ninokura et al., 2004), especially given its direct connection with the basal ganglia (Alexander et al.,

1986; Maurice et al., 1999). While both chunks and sequence identity are reliably encoded in areas of the premotor and parietal cortex, these regions did not distinctively represent these features when measured using fMRI (Yokoi and Diedrichsen, 2019). Thus, it is unclear whether these regions play similar or distinct roles in the sequence hierarchy. To get a better grasp of the hierarchical control of movement sequences, it will be important for future studies to investigate the temporal dynamics of the neural activity during sequence execution alongside the spatial distribution of it. This will not be trivial, however, given the drawbacks of different imaging techniques.

4.2.2 Changes in hierarchical representation with training and its relationship to performance

Previous research has suggested a link between the extent to which a movement sequence is hierarchically organized and the skill level at which it is performed (Bläsing et al., 2009; Schack and Mechsner, 2006; Velentzas et al., 2010). Frank and colleagues (2016, 2013) suggest that increases in performance prompt a build-up of hierarchical organization, as novices show less hierarchical organization compared to experts (Bläsing et al., 2009; Schack and Mechsner, 2006; Velentzas et al., 2010). I argue that these two processes are mediated through performance variability resulting from increased exploration early in training. In **chapter 2** we demonstrated that early in practice, the chunking structure of participants in the control group varied highly from trial to trial. This variability decreased with training, becoming more similar to the experimental group. This early exploration might present itself as reduced hierarchical clustering when analyzed using the Structural Dimensional Analysis of Mental Representation (SDA-M) by Schack and colleagues. Increased motor variability has been proposed to benefit learning (Adi-Japha et al., 2008; Dhawale et al., 2017; Wu et al., 2014). Hence, settling on a particular hierarchical organization too early might result in reduced exploration (Uehara et al., 2019), and subsequently worsens performance (Lee and Ranganathan, 2019). In summary,

the lack of hierarchical organization observed in novices potentially reflects greater exploration of chunk patterns early in training. Future studies could correlate the differences in inter-individual exploration with measures of hierarchical clustering, and relate those to subsequent performance outcomes to disentangle the influence of each of these behavioural measures on the hierarchical organization.

While there is a lack of hierarchical organization early in training, both of our studies show a clear hierarchical organization after extensive practice. One innovation of our study in **chapter 2** was that we directly manipulated participants' early sequence representation. This provided a stronger manipulation to estimate the relationship between hierarchical organization and performance at the end of training. Thus far studies have predominantly observed the relationship between hierarchical organization and performance as it naturally unfolded (Bläsing et al., 2009; Schack and Mechsner, 2006; Velentzas et al., 2010). In our experiment, we manipulated participants' early sequence representation to be functionally beneficial or detrimental to performance, providing a unique window to assess how these instructions subsequently influenced performance. While instructions shaped performance throughout training, participants who were able to abandon the disadvantageous performance pattern we induced, managed to improve their performance. If the disadvantageous instructions were not overcome, participants' performance remained suboptimal. Thus, we provide evidence for a direct link between participants' representation and performance level after extensive training.

4.2.3 The necessity of instructions for a beneficial hierarchical organization

In **chapter 2** we found that the control group, which received no instructions, naturally moved closer to the beneficial chunk structure with training and showed similar results in terms of crystallization, chunk concatenation, and overall

performance speed as the experimental group. Combined with our previous finding that detrimental instructions can harm performance long-term, one could question whether providing instructions might be more harmful than useful for the formation of mental representations and subsequent performance.

Indeed, several studies have reported that participants who learned a task without instructions, commonly referred to as “discovery learning”, showed similar (Berry and Broadbent, 1984; Hodges and Lee, 1999; Meier et al., 2020) or even better performance (Vereijken and Whiting, 1990; Wulf and Weigelt, 1997) compared to participants provided with instructions. Meier and colleagues (2020) tracked how instructions affected performance and mental representation of participants’ volleyball serve over five weeks. Participants who received instructions shifted their mental representation closer to the optimal structure. However, this change did not lead to significantly better performance compared to a control group who did not receive instructions. These results suggest that instructions are not superior to discovery learning. Researchers investigating the potentially harmful effects of instructions on performance, emphasize the increased memory load and attention demands (Green and Flowers, 1991). Such accounts argue that the retrieval of instructions might be interfering with automatic processes needed to enhance performance (Wulf et al., 1998). However, our finding that a reduction in the cognitive load (by switching from a memory-guided to a visually-guided task mid-way through training) did not influence participants’ chunk structure or overall performance, opposes this idea. Furthermore, multiple studies have provided evidence that favour instructions over the use of discovery learning to improve performance (Al-abood et al., 2001; Alfieri et al., 2011; Nigam and Klahr, 2004).

In summary, while it is possible to achieve a functionally beneficial hierarchical representation without instructions, it is important to understand what boundary conditions might mediate the effectiveness of discovery learning over instructions. Potential factors could include task complexity, the age of the learner (Alfieri et al., 2011), or prior task knowledge (Gijlers and De Jong, 2005).

As different types of discovery learning have started to be applied in classrooms (Balım and Günay Balım, 2009; Nigam and Klahr, 2004), it is important to get a better grasp on what task parameters determine which of these two teaching modes is superior in a given context.

4.3 Mechanisms underlying the natural emergence of hierarchical organization

As evidenced by our control group (**chapter 2**) and previous research (Verwey, 1996; Wymbs et al., 2012), a hierarchical organization, as behaviourally represented by chunking, arises naturally with training. It is still unclear, however, what mechanisms underlie the structure of these naturally emerging chunk patterns. In **chapter 1,** I discussed how finger patterns, as well as temporal and visual presentation characteristics, can impact sequence segmentation (de Kleine et al., 2009; Koch and Hoffmann, 2000; Verwey and Eikelboom, 2003). This suggests that structural regularities might play a key role in the formation of chunk patterns.

It has been found that humans are able to extract structure from sequences without the need for instruction or conscious awareness (Conway and Christiansen, 2005; Fiser and Aslin, 2002; Saffran, 2001). Even young children can extract structural regularities from speech streams (statistical learning; Saffran et al., 1996). One prominent task that has been used to assess this ability is the artificial grammar learning task (Reber, 1967). In artificial grammar learning tasks, participants are first presented with sequences of letters. Afterwards, they are made aware that the sequences followed a particular grammar rule but are not informed about the specific rule. They are then asked to determine whether novel sequences of letters follow the same rule. These types of studies have demonstrated that participants are surprisingly good at extracting statistical probabilities of sequence transitions without being explicitly instructed

to uncover the rule. It has been suggested that chunking could arise through this sensitivity to statistical regularities.

4.3.1 Possible mechanisms underlying chunk formation

Three possibilities have been postulated regarding the interaction between the statistical regularities in sequences and chunk formation (Perruchet and Pacton, 2006). First, chunks are formed through a random process that is not informed by the statistical regularities (e.g., through a random process), but can subsequently be modulated by them (Perruchet and Pacton, 2006). Second, chunk formation and the learning of statistical regularities are independent processes (Meulemans and Van Der Linden, 2003). And third, chunk boundaries are driven by the statistical regularities in the sequence (Beukema and Verstynen, 2018).

Support for the idea that chunking occurs randomly but is then governed by statistical processes comes from two models in the artificial grammar learning field: PARSER (Perruchet and Vinter, 1998) and the Competitive Chunk model (Servan-Schreiber and Anderson, 1990). Both of these models suggest that sequences are initially parsed into chunks through a random process. These chunks are then either strengthened or forgotten based on whether they are repeated in future executions (through regularities/frequencies). Both models have been shown to explain participants' performance during artificial grammar learning (Boucher and Dienes, 2003; Perruchet and Vinter, 1998).

As an alternative proposal, Meulemans and Van Der Linden (2003) argue that chunking and the learning of statistical regularities (i.e., association mechanisms) are two independent processes. They found that amnesic patients performed akin to a control group in the classification of novel sequences during an artificial grammar learning task. However, when participants had to generate strings that agreed with the grammar rule, control participants outperformed amnesic patients. They argue that chunk knowledge is explicit and thus

necessary for sequence generation, while recognition is governed by implicit processes and proceeds without the need for chunk knowledge.

Studies in motor sequence learning have also started to distinguish these possibilities. In a continuous serial-reaction time task (SRTT; Nissen & Bullemer, 1987), chunking was found when the stimuli had structural characteristics (Jiménez, 2008; Koch and Hoffmann, 2000), such as ascending and descending finger patterns. However, Jiménez (2008) highlighted that these chunk structures could be explained by biomechanical constraints. As discussed in **chapter 2,** biomechanical factors can influence performance, and therefore might have driven the chunking observed in the study by Koch and Hoffmann (2000). Du and Clark (2017) considered these biomechanical constraints during an SRT task by removing the slow and fast reaction time components that were periodically repeated in the sequence. They found that chunking subsequently vanished and performance was best characterized by first-order autocorrelations. However, measuring biomechanical constraints on the same data that is used for analyses could lead to biased results. In **chapter 2** we presented a more unbiased way of considering biomechanics, by measuring them separately from the main experiment and building up a general biomechanical profile that was then used to remove these features from our experimental data. Using this cleaner approach to account for biomechanical constraints, we still observed clear chunking patterns throughout training.

4.3.2 Investigation into chunk versus statistical regularities

In work that is not included in the previous thesis chapters, we tried to get a better grasp of the distinction between chunking and learning of the statistical regularities in the acquisition of finger movement sequences.

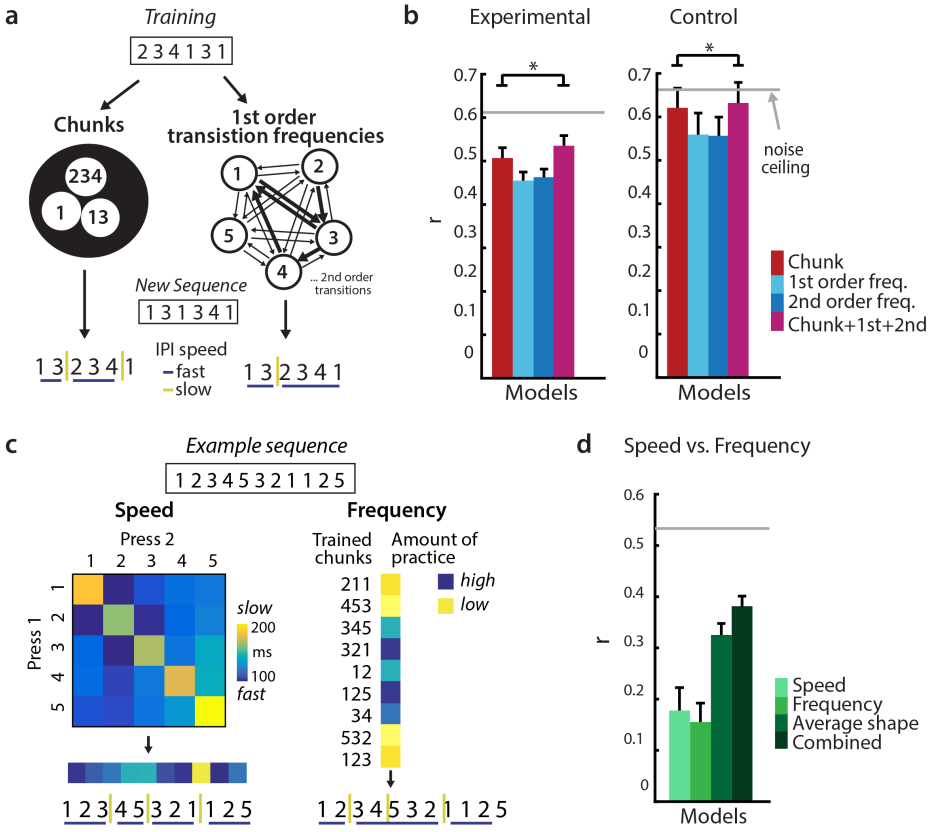
We first addressed this question by reanalyzing data from **chapter 2** to investigate whether participants' chunk pattern was not only driven by our

instruction but also by statistical regularities (**Figure 4.2a**). To do so, we used cross-validated regressions to compare how well different statistical and chunk properties predicted participants' inter-press intervals (IPIs). For the experimental group, a combined model of chunk and transition frequencies best predicted the data, suggesting that even though we instructed their chunk structure, statistical properties still seemed to drive some of the inter-press interval patterns we observed (**Figure 4.2b**). For the control group, we predicted participants' most likely chunk structure using our Bayesian algorithm discussed in **chapter 2** and again found that a combination of frequency of transitions and chunk pattern best described behaviour (**Figure 4.2b**). Therefore, our data reinforce the idea that both of these processes contribute to participants' behaviour. However, because this task was not designed to systematically differentiate between these models, we are unable to make any further claims regarding the interaction between them.

Next, we designed an experiment to test whether participants' chunk pattern, is better explained by the frequency of exposure or by the speed with which participants could execute the different transitions (**Figure 4.2c**). If a hierarchical representation that is beneficial to performance is indeed formed naturally, one could expect the resulting chunks to be based on execution speed rather than on frequency of exposure. In this manner, the hierarchical representation is constructed to achieve the fastest performance given certain task and working memory constraints. Akin to the experiment in **chapter 2**, we initially had participants produce two, three or four-keypress combinations for two days. We carefully manipulated the frequencies with which these transitions were performed. Participants were then exposed to longer sequences across two additional days. These sequences were designed to produce particular IPI patterns depending on which a priori model was followed. On the first and last day of practice, we included a session where participants performed all possible two-press transitions (e.g., 1-2, 1-3, … 4-5). This data was used to form a biomechanical baseline measure for each participant, which was in turn used to predict the speed of the transitions (**Figure 4.2c**). The two central models that we

used for our predictions were: 1) that participants' inter-press interval pattern followed the pre-trained transitions based on the frequency with which they were exposed to them; 2) or that participants' inter-press interval pattern was driven by the speed with which they could execute the pre-trained press combinations. We also considered other nuisance models such as the average shape of the IPI pattern across the sequence, to account for the observation that we see a speedup of execution at the beginning and end of the sequence with slowing in the middle ('average shape' in **Figure 4.2d**). Our analyses revealed that none of the models (alone or in combination) accounted for the observed behaviour to a satisfactory degree (when compared to the noise ceiling; **Figure 4.2d**). This tells us that there is structure in participants' behaviour that our models could not account for. The variance that we could not predict with our models could either 1) stem from nuisance variables that impact chunking, or 2) could be the result of an underlying mechanism that we missed to include. Furthermore, two days of sequence training might have not been enough to form stable IPI patterns in all participant

Figure 4.2. Statistical regularities versus chunk learning.
(a) Distinction between a chunk model and a model based on the frequency of transitions. Based on participants' exposure to different transition frequencies and chunks we can make distinct predictions regarding the inter-press interval (IPI) pattern of novel sequences. Dark blue in both instances represents faster execution, whereas yellow represents chunk boundaries/longer IPIs. Error-bars denote the between-subject standard error. **(b)** Prediction results for the experimental and control group based on data from week 3. For both groups a combination of chunking and 1st (press transition between two press, i.e., 1-2) and 2nd (press transitions between 3 presses, i.e. 1-2-3) order transition frequencies best fit the data. The noise ceiling represents the variance in participants' behaviour that the models should be able to explain. **(c)** Abstract representation of how we can predict a distinction in IPI patters between a model that is based on the speed of the press combination or based on the frequency of exposure. The speed estimation for the IPI prediction was based on the biomechanical baseline (all press transitions) of the participant on day 1. The frequency prediction was based on the occurrence of the transition(s) during the practice, with a high frequency resulting in faster IPIs. **(d)** Results from the regression analyses. A combination of all three models did not reach the noise ceiling. The average shape model considers the overall speed changes across sequence execution. The combination model combines all three models. Error-bars denote the between-subject standard error.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Models

Previous research, including the work in this thesis, has demonstrated that testing the underlying mechanism of naturally occurring chunking patterns has proven difficult. One difficulty arises from the type of statistical regularities that are considered. A few studies have primarily focused on the frequency of occurrence of each element (Chang and Knowlton, 2004; Servan-Schreiber and Anderson, 1990) while ignoring other measures that play important roles, such as the first or second-order transition frequency (Fiser and Aslin, 2002; Hunt and Aslin, 2001). Hence, it is important to investigate a variety of different types of statistical measures to be able to create more accurate models.

As experienced by myself, designing a sequence experiment that predicts differences in behaviour between specific a priori models requires a greater amount of work early in the project before data collection can begin. The statistical properties of strings of letters, numbers, or presses are often entangled with each other and with chunk measures (Perruchet and Pacton, 2006). For instance, the frequency of chunk occurrence also affects the first-order transition probabilities. Hence, to provide systematic insights into differences between learning of statistical properties and chunking, future studies should follow in our footsteps and determine whether their experimental design can theoretically distinguish between possible models.

Lastly, exposure outside of the experimental setup (e.g., different languages or musical experiences) likely influences chunking patterns and the resulting mental representations. This can lead to inter-individual differences that are hard to control for and difficult to account for (Perruchet and Gallego, 1997). While we want participants to chunk sequences naturally to get an unbiased estimate, we need consistent behaviour across participants to make strong inferences. Therefore, to avoid high inter-individual variability we either have to bias participants' performance via pre-training, or use sequence structures that naturally produce specific behavioural patterns.

4.4 Changes in feedback use with training

In **chapter 3** we found that participants still adjusted their behaviour in accordance with the feedback perturbation after four days of training, albeit to a lesser extent than at the beginning of training. This suggests a shift from feedback to feed-forward control with practice, which has been related to increased automaticity and more accurate internal models (Jordan and Rumelhart, 1992; Wolpert et al., 1995), resulting in less reliance on feedback during execution (Seidler-Dobrin and Stelmach, 1998). Our findings align well with hybrid models of motor control (Desmurget and Grafton, 2003, 2000; Hoff and Arbib, 1993; Pélisson et al., 1986; Wolpert et al., 1995) in which sensory feedback is integrated and compared to a predicted state. If this comparison leads to a discrepancy, a corrective signal is sent to correct the ongoing movement. While our findings from **chapter 3** reinforce a shift from feedback to feed-forward control, the mechanism responsible for attenuating the impact of the sensory feedback with training is uncertain. Below, I will elaborate on two possible mechanisms that could explain the observed shift.

4.4.1 Sensory attenuation through an increase in self-agency

One possibility is that the sensory information is reduced through sensory attenuation. This mechanism represents the process by which we filter afferent information to limit the amount of received feedback (Blakemore et al., 1998). Sensory attenuation is originally thought to help distinguish self-motion from externally-caused motion (Shergill et al., 2003) and is said to arise from internal model computations. The sensory prediction from the feed-forward model is compared to the received feedback; if these two match, the sensation is attenuated (Wolpert and Ghahramani, 2000). For instance, the inability to tickle oneself has been explained via sensory attenuation (Blakemore et al., 1998, 2000). I argue that an increase in sensory attenuation potentially underlies the reduction in feedback perturbation effects we observed in **chapter 3**. Two

interconnected factors are supposed to play a role in increasing sensory attenuation: the sense of self-agency and intentional binding.

It has been demonstrated that an increase in the perception of self-agency results in increased sensory attenuation, while the opposite is true for decreasing sense of self-agency (Desantis et al., 2011; Kilteni and Ehrsson, 2017; Moore et al., 2009). Increases in the accuracy of internal models have been suggested to inflate the sense of self-agency (Blakemore et al., 2000). Therefore, training-induced changes in the accuracy of internal models can enhance the perception of self-agency and in turn result in greater sensory attenuation.

However, temporal delays between the action and the subsequent sensory consequence have been shown to reduce the perception of self-agency (Blakemore et al., 1999). Therefore, our experimental manipulation of inducing a sensory delay or advancement to the sensory consequence of the action would predict a decrease rather than an increase in sense of agency. Nevertheless, it has been shown that participants adapt to a delay in sensory consequence with training. For instance, electroencephalography (EEG) patterns produced by tones that were delayed by 100 ms after movement onset were shifted with training to become more similar to the EEG patterns when feedback was synchronous with the movement (Cao et al., 2017; Elijah et al., 2018, 2016). This suggests a learned adjustment in temporal prediction (Stetson et al., 2006; Timm et al., 2014), by reducing the perceived delay between the action and the sensory consequence. This temporal binding between an action and its delayed sensory consequence has also been termed intentional binding (Haggard et al., 2002). It is therefore possible that in our experiment the motor system adjusted its temporal prediction window with training to include the small feedback perturbations that we induced. This increase in intentional binding would allow for an increase in self-agency with training. And in turn, this increase in self-agency would prompt greater sensory attenuation, which we observed as a reduction in behavioural effects from the feedback perturbations.

4.4.2 Learning to ignore external perturbations

Another mechanism by which participants could have reduced the effect of the feedback perturbation is through learning that the perturbation was irrelevant to performance (Diedrichsen et al., 2005). Our task was designed so that participants did not need to wait for the delayed feedback to occur to move on to the next press. Therefore, it is possible that through training the motor system realized that the feedback perturbations are not directly related to performance. Wei and Körding (2009) demonstrated that the motor system indeed estimates whether the error directly relates to movement production. Thus, if the perturbation is believed to be driven by external factors that are not under one's control, this should reduce the behavioural adjustments. In contrast to the previously discussed mechanism, in this proposal participants assign less agency to the perturbed feedback with training. It has previously been suggested, however, that error-sensitivity increases with training (Herzfeld et al., 2014), which would suggest that we become more sensitive to the sensory perturbation with training. Nevertheless, a recent study found that this was only the case in highly consistent environments. If the variability of the perturbation magnitude was high during a motor adaptation task the increase in error-sensitivity with training was stunted (Albert et al., 2021). This finding potentially reinforces the idea that participants did not become more sensitive to errors with learning, but rather decreased their overall sensitivity to the perturbations.

While we cannot be certain about the mechanism that drove our results, one way to possibly dissociate these two mechanisms in the future is by slightly increasing the feedback perturbation (i.e., temporal delay) after a certain amount of training. If we assume that learning to ignore perturbations is a general process with a broader impact, we would expect that the behavioural adjustments to the increased perturbation should be similar to the previously experienced perturbation. In this scenario, the motor system should have learned to ignore a broad range of external feedback perturbations. On the other hand, if we assume that in the sensory attenuation scenario the temporal prediction

window is only increased to the extent of the largest experienced perturbation, then we would expect greater behavioural adjustments to the increased perturbation compared to the previously experienced perturbation. Nevertheless, this test assumes that learning to ignore a perturbation generalizes to multiple perturbation sizes, which might not be the case.

4.5 The issue of task fragmentation and its impact on generalization and validity

When first designing a new experiment, the overarching goal is to produce results that provide strong evidence for or against a certain theory or hypothesis ("Dogmas, paradigms and proving hypotheses," 2010). In a perfect world, we wish to make strong claims that are relevant and generalize to all sequential movements. In reality, however, results are often messy, not straightforward, and deviate from initial expectations. Nevertheless, to publish, they need to be perceived as polished, novel, and generalizable (Franco et al., 2014). While this exposes issues in publication requirements, which have been discussed elsewhere (Franco et al., 2014; Mlinaric et al., 2017; Rockwell et al., 2006; Rosenthal, 1979; Yong, 2012), it also relates to the idea of "task fragmentation" (Ranganathan et al., 2021), which I will address next. In this last section of my discussion, I aim to offer some suggestions on this broader issue that I have been confronted with during my dissertation research.

4.5.1 Task fragmentation

The paradigm we use is often specific to the research lab, meaning that the likelihood of another lab using the same experimental setup is small or negligible. This leads to a high volume of paradigms with very little overlap between them (Ranganathan et al., 2021; see Yartsev, 2017 for an opposing view in animal models). Even if the same task is used, the difference in exact measures and

equipment can lead to discrepancies in outcomes (Ranganathan et al., 2021). For instance, in finger sequence tasks some research groups including ours use keyboard-like devices while others use computer keyboards or button boxes. This can lead to differences in finger placements and forces that need to be produced. Usually, we try to explain discrepancies in results by pointing out differences between tasks. We do so to reinforce the validity of our results and blame external circumstances for any differences. This process is similar to the self-serving bias in psychology (Miller and Ross, 1975; Taylor and Doria, 1981), where success is personal and failures are situational. We tend to ascribe discrepancies in results between our and other studies to experimental factors that were likely chosen out of convenience or based on arbitrary measures (Ioannidis et al., 2014). For instance, the size of feedback delay in **chapter 3** was primarily chosen so that it was not consciously perceived by the majority of participants. However, the exact sizes that were chosen are arbitrary and were on average larger in contrast to similar studies (Repp, 2000; Wing, 1977). These types of discrepancies make comparisons between studies difficult. While disagreement and disproval play key roles in science advancement (Bauerlein, 2002; Dellsén and Baghramian, 2020; Kuhn, 2012; Lugg, 1978; “The power of disagreement,” 2016), how can we possibly evaluate which of such contradictory findings is “more valid” when differences are attributed to minor technical details (Smalheiser, 2013)? And how can we ultimately decide on overarching processes that can account for the discrepant outcomes (Collins, 2009; Muthukrishna and Henrich, 2019)?

4.5.2 Discrepancies as opportunities

One way we could use task fragmentation to our advantage is by taking an experimental approach when considering the discrepancies in results. In my experience, and I am guilty of it as well, differences are often half-heartedly addressed in the discussion section, with the knowledge that they will likely not be experimentally addressed in the future. It could, however, be valuable to put

greater effort into understanding the factors we believe underlie the discrepancies. As my supervisor would often say to me “a gut feeling is good but not sufficient”, as long as the gut feeling is not critically tested it remains just a “feeling”. Therefore, we should attempt to experimentally characterize what we believe caused these differences. For instance, in **chapter 3**, we could repeat the same experiment but instead of having participants perform the sequences as fast and accurately as possible, we could ask them to synchronize their movements to an external variable. This way we can test for behavioural differences that are related to the task goal and better link our findings to the synchronization literature. Treating the differences in results as an opportunity rather than as a “necessary evil” could promote generalization even with fragmented task designs.

4.5.3 Model tasks

To overcome the issues of the fragmentation of tasks, Ranganathan and colleagues (2021) suggested to introduce “model tasks” that are formally operationalized and are related to particular paradigms used in motor neuroscience (e.g. adaptation). By constraining and formalizing the specific variables and equipment to be used, generalizability across research labs increases. For instance, a “model” sequence task might use a standard computer keyboard combined with a specific computer screen and clear instructions regarding the complexity and length of sequences of letters that are to be used. This could provide a standard setup for finger sequence tasks that is cost-effective and easy to implement. The study in **chapter 2** could easily be replicated using such a setup. However, how many of these model tasks would we need to include a variety of movement sequences. While findings from finger sequence tasks can potentially approximate processes involved in piano playing or typing on our laptops, we would like to generalize our findings to other movements that we make in our daily life, such as making a cup of coffee or hitting a baseball. Model tasks enable a narrow increase in generalization within

a certain task category, they do not, however, address the issue of generalizing to broader categories.

A further issue that could be mediated using model tasks is replication (Camerer et al., 2018; Open Science Collaboration, 2015). Replication is important to reinforce previous findings (Harzing, 2016; Zwaan et al., 2017). However, replications, similar to null results (Mlinaric et al., 2017), are often not exciting enough to warrant a publication without the inclusion of exciting new findings (Pashler and Harris, 2012). With model tasks, replication will be pushed to the foreground and small changes in the model variables can still lead to novel results (Ranganathan et al., 2021).

The idea of “model tasks” is intriguing in the current climate of task diversity; however, it opposes the ingrained idea of scientific freedom (“AAAS Statement on Scientific Freedom and Responsibility,” 2017; Simmons et al., 2011; Wilholt, 2010). While task fragmentation results in many findings that are hard to consolidate, it allows for creativity and exploration. Model tasks would reduce this freedom by constraining it. This leads to a more philosophical question: Would the field become complacent and stagnant if novel findings would not constantly make us question our previous beliefs? Humans are creatures of habits that crave consistency and dislike change (Carden and Wood, 2018; Ersche et al., 2017; Marien et al., 2018). Maybe the variety in findings and experimental setups bolsters our critical thinking and discourages complacency. To sum up, model tasks provide an interesting way to address some of the issues regarding generalization, reliability and validity of research findings, however, given some of the drawbacks they might not come into realization in the near future.

4.5.4 Changes in experimental designs to promote generalization

Instead of revamping the entire system, changing how we collect and compare data could also lead to greater generalization irrespective of task fragmentation. Generally, we try to generalize from a small subset of participants to a population. However, given the frequently small sample sizes in neuroscientific research (Nee, 2019; Turner et al., 2018), this type of generalization might not always be valid (Button et al., 2013; Ranganathan et al., 2021; see Smith & Little, 2018 for an opposing view). While some collaborative projects across labs and countries have achieved larger participant samples (Van Essen et al., 2013; Volkow et al., 2018), this is not always possible. Therefore, I want to address another way by which we could improve generalization given task fragmentation and small sample sizes.

Instead of focusing on the participant sample size, we could focus on the stimuli we are using. To potentially improve generalization, we could diversify the stimuli set that we present to participants. Instead of providing the same stimuli to all participants, it might be valuable to provide each participant with a unique set of stimuli. For instance, when investigating differences in the neural representation of trained and untrained sequences, instead of training all participants on the same set of sequences, each participant trains on a distinct set that does not overlap with other sets. While this will likely increase between-subject variability, because of the variation in stimuli, the overlapping effects we find are potentially more generalizable across the stimuli category. This design choice is possible if the stimuli pool is large, but becomes difficult when only a few stimuli are associated with a category. Nevertheless, this experimental design reduces the random effects associated with using specific sets of stimuli.

Instead of tinkering with the overall experimental design to account for stimuli specificity, adjusting the assignments of fixed and random effects in statistical testing can also improve generalizability. It has been proposed that stimuli variability should be considered as a “random-effect” rather than as a “fixed-effect” to overcome the issue of generalizing effects that stem from limited

sets of stimuli (Chang and Lane, 2016; Judd et al., 2012; Westfall et al., 2017). While there is no single right answer to how research should promote generalization, it is important to be aware and vigilant of this issue.

4.6 Conclusion

In summary, the research presented in this thesis demonstrates that skilled finger sequences are represented hierarchically and are adjusted continuously to incoming sensory feedback. We provided new evidence on the causal relationship between sequence representation and skill level by manipulating early sequence representation through instructions. Our results demonstrate the continuous integration of sensory feedback during finger movement execution even after extended practice. Additionally, we observed a shift from feedback to feed-forward control with training. Our results reinforce a hybrid control model of motor control that uses a combination of feed-forward and feedback control to adjust ongoing movement execution. Overall, this thesis provides novel insights into the representation and control of finger movement sequences.

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Appendices

Appendix A: Questionnaire given to subjects in the study in Chapter 3.

Subj: **Study: Sequence Integration 4**

Questionnaire about Experience:

Did you notice anything during the experiment?

We manipulated an aspect of the task during the experiment what was it?

Which of these manipulations did we implement (chose any that apply)?

- ☐ Change the frequency of the tones that were presented when a key was pressed
- ☐ Delay the feedback of a press
- ☐ Provide false feedback on a press (if you were correct it would show as incorrect)
- ☐ Interleave the 3 trained sequences with random sequences
- ☐ Change the frequency of the vibration when a key was pressed
- ☐ Advance the feedback of a press
- ☐ Switched a single press within the sequence (switch which number is presented)
- ☐ Randomize the points you received for each trial rather than making them dependent on performance
- ☐ Omit the feedback of a press
- ☐ Give you false feedback regarding your average speed at the end of a block (higher or lower than you actually were)

Appendix B: Letter of information and Consent Form for experiments for Chapters 2-3

LETTER OF INFORMATION FOR PARTICIPANTS

Studies of the acquisition and control of skilled finger movements

Principal Investigator:
Jörn Diedrichsen, Ph.D.
Departments of Computer Science and Statistics
University of Western Ontario, London, Ontario
[redacted]

Introduction
We would like to invite you to take part in an observational study in motor control. The purpose of the research is to determine how complex movement skills are learned and controlled. You are being asked to participate in this research, because we recruit participants without neurological disorders, with two functional upper limbs and with normal or corrected-to-normal vision. You should participate in this study only if you want to; you are not required to in any way. Before you decide whether you wish to take part, please read the information below. Please ask us if anything is unclear or you would like more information.

Research Procedures
If you agree to participate in this study, you will undergo multiple training and testing sessions. We will schedule the sessions during days that are most convenient for you. These sessions will involve behavioral training in the laboratory in the Brain and Mind Institute located in the Western Interdisciplinary Research Building on Perth Drive.

In these sessions, you will be seated in front of a finger box, which resembles a piano keyboard, and a monitor. You will be asked to make a sequence of key presses in a pre-specified order as quickly as possible – sometimes you also have to press multiple fingers at once in a coordinated pattern. The finger box will record the movement and force of each finger.

In some experiments, we might attach a number of adhesive electrodes to the surface of your skin to record your muscle activity. These electrodes will only be used for recording and never for stimulation. In other experiments you may be asked to look at the screen through an eye tracker, so that we can record the movements of your eyes. This will simply be done by resting your chin on the eye-tracker's chin rest.

After each activity, you will receive visual and/or auditory feedback on speed and accuracy. The testing is organized into blocks of trials of 3-6min length. After each block you will have the opportunity to take a break. Each session may take up to 2 hours. You may be asked to come to the testing centre for a single session or multiple sessions depending on which experiment you are completing.

We anticipate enrolling 400 participants in total, with approximately 20 versions of the experiment involving 6 - 20 participants each. The research staff will let you know which experiment you will be completing as well as the expected duration and number of sessions involved at the time of consent.

Risks
The study has basically the same level of risk as working at a computer keyboard or practicing a musical instrument. The main risk is fatigue in the hand from the repetitive movement. The experimenter will offer you opportunity to take breaks during the experiment as often as you wish.

Benefits and compensation
There is no direct benefit to you from participating in this study. The results from this study may help us to better understand the brain regions underlying human motor learning.

You will be compensated for each session you attend, and will receive $10 for every hour of participation. Additionally, you will receive bonuses based on your performance during the motor task. On average the additional reward will be $5 an hour. If the study has to be stopped for any reason, compensation will be adjusted according to the fraction of the study that was completed.

Voluntary Participation / Withdrawal from Study
You should only participate in the study if you really want to; choosing not to take part will not disadvantage you in any way. At any time during the study, the experimenter may ask you to stop the study. This usually occurs for technical reasons. You can withdraw from the study at any point in time if you feel uncomfortable or tired –you just have to tell the experimenter that you wish to stop. Withdrawal will have no negative consequence for you or your academic status, and you will be paid for your time that you have spent on the experiment up to that point. You can also withdraw your data from the study at any time, without negative consequence for yourself, your academic status, or your reimbursement.

At a future date, we may ask whether you would be willing to participate in an additional study from our lab or institute. If you are interested in participating, please check and initial the "Contact for Future Studies" section on the Consent Form. You may freely decline to participate in any future studies and to be contacted further.

Confidentiality
Any information obtained from this study will be kept confidential. Any data resulting from your participation will be identified only by a participant code, without any reference to your name or personal information. A sheet linking you name to the participant code will be stored in a securely locked filing cabinet in a room that will be accessible only to the experimenters. Seven years after completion of the study these records will be destroyed. Representatives of the University of Western Ontario Health Sciences Research Ethics Board may require access to the study-related records or may follow up with you to monitor the conduct of the study. De-identified data will be kept past these seven years for future usage.

Name of Sponsor / Conflict of Interest
The research is supported by a startup grant from Western University, and a Scholar award from the James S. McDonnell Foundation. Neither of the funders has played any role in study design or analysis. None of the **Investigators has a financial interest in the outcome of the study.**

Consent Form
You do not waive any legal rights by signing the consent form. If you wish, we can provide you with a copy of this letter of information and the consent form.

Contact Information
A more complete and detailed description of the study is available from the principal investigator, Professor Jörn Diedrichsen [redacted] Professor Diedrichsen will try to answer any questions that you may have.

If you have any questions about your rights as a research participant or the conduct of the study you may contact:

The Office of Research Ethics
Western University
[redacted]

CONSENT FOR RESEARCH STUDY

Studies of the acquisition and control skilled finger movements

I have read the letter of information, have had the nature of the study explained to me, and I agree to participate. All questions have been answered to my satisfaction.

Dated in London, this_____ day of_____,20___.

Name of Participant (Please print): _____

Signature of Participant: _____

My signature means that I have explained the study to the participant named above. I have answered all questions.

Signature of Person Responsible
for Obtaining Consent:_____

Name of Person Responsible
for Obtaining Consent (Please print):_____

Date for Obtaining Consent: _____

Contact for Future Studies

Please check the appropriate box below and initial:

☐ I agree to be contacted for future research studies

☐ I do NOT agree to be contacted for future research studies

Curriculum Vitae

Nicola Popp

Education

09/2016 – present	**University of Western Ontario** **London, Canada** PhD in Neuroscience Supervisors: Paul Gribble, PhD and Jörn Diedrichsen, PhD
03/2016 - 08/2016	**University of Western Ontario** **London, Canada** Visiting Research Student Supervisor: Jörn Diedrichsen, PhD
11/2014 - 7/2015	**Johns Hopkins University School of Medicine** **Baltimore, USA** Master's Thesis research internship Supervisors: John Krakauer MA, MD and Adrian Haith, PhD
2013 – 2015	**Maastricht University** **Maastricht, The Netherlands** Research MSc in Cognitive and Clinical Neuroscience, completed with distinction
2010 – 2013	**University of Groningen** **Groningen, The Netherlands** BSc Psychology, completed with distinction
9/2012 - 12/2012	**Queen´s University** **Kingston, Canada** Exchange Student

Honors and Awards

2017, 2018 and 2019	Western Neuroscience Graduate Program Travel Award, $500
2018	CoSMo summer school travel award (1,500 CAD)

2016-2020	Western International Graduate Student Scholarship ($60,000 CAD total over 4 years)
2015	Nomination Annual Dutch MSc Thesis Award for Cognitive Neurosciences (one thesis nomination per university)
2014	Grant from the Limburg University Fund (SWOL), 500€
2014	FPN Grant from the Maastricht University, 700€
2012	Marco Polo Scholarship from the University of Groningen, 700€

Experience

9/2020 – 4/2021	Teaching Assistant, Introduction to Psychology, University of Western Ontario
9/2019 – 04/2020	Proctor, Department of Psychology, University of Western Ontario
9/2019 – 12/2019	Teaching Assistant, Neuroimaging of Cognition, University of Western Ontario
1/2019 – 4/2019	Teaching Assistant, Cognitive Science Course, University of Western Ontario
9/2017 – 4/2018	Teaching Assistant, Psychology Honours Thesis Course, University of Western Ontario
9/16 – 4/17	Teaching Assistant, Introduction to Psychology, University of Western Ontario
11/2015 – 1/2016	Research Assistant at the Sensorimotor Group, Cognitive Neuroscience Laboratory, German Primate Center Supervisor: Alexander Gail, PhD
7/2014 - 10/2014	Research Assistant at the Department of Cognitive Neuroscience, Maastricht University Supervisor: Amanda Kaas, PhD

Publication

Popp N. J., Yokoi A., Gribble, P. L., & Diedrichsen, J. (2020). The effect of instruction on motor skill learning. Journal of Neurophysiology, 124, 5, 1449-1457.

Berlot, E., **Popp, N. J.**, Grafton, S. T., & Diedrichsen, J. (2020). Discrepancy between repetition suppression and pattern analysis provides new insights into the role of M1 and parietal areas in sequence learning. bioRxiv.

Berlot, E., **Popp, N.J.**, & Diedrichsen, J. (2020). A critical re-evaluation of fMRI signatures of motor sequence learning. Elife, 9, e55241.

Berlot, E., **Popp, N.J.**, & Diedrichsen, J. (2018). In search of the engram, 2017. Current Opinion in Behavioral Sciences, 20, 56-60.

Oral Presentation

Popp N.J. & Yokoi, A., Diedrichsen J. & Gribble P. L. (2017). Bad habits: how initial instructions influence performance in long-term motor sequence learning. Advances in Motor Learning & Motor Control 2017" (MLMC). Satellite meeting of the 47th annual meeting of the "Society for Neuroscience" (Washington, USA)

Poster Presentation

Popp N.J., Gribble, P. L. & Diedrichsen, J. (2019). The use of sensory feedback during the production of fast motor sequences. Neuroscience 2019 (Chicago, USA)

Popp N.J., Kordjaz, N., Gribble, P. L. & Diedrichsen, J. (2018). Evidence for chunking vs. statistical learning in motor sequence production. 2018 conference on "Cognitive Computational Neuroscience" (Philadelphia, USA)

Popp, N.J., Yokoi, A., Gribble, P. L. & Diedrichsen, J. (2017). Bad habits in motor skill learning: how initial instructions influence performance in long-term motor sequence learning. 27th Meeting of the "Society for the Neural Control of Movement" (Dublin, IRL)

Popp, N.J., Harper, M. & Haith, A.M. (2016). Retrieval of a motor memory triggered by a previously unseen error. 46th annual meeting of the “Society for Neuroscience" (San Diego, USA)

Popp, N.J., Wong, A.L., Haith, A.M. & Krakauer, J.W. (2015). Switching between motor plans of simple and complex movements. 25th Meeting of the “Society for the Neural Control of Movement” (South Carolina, USA)

Science Outreach

London Brain Bee Competition 2017 - 2020 – primary organizer

Western Undergrad Psychology Journal 2017-2020 - graduate editor

Thames Valley Science & Engineering Fair 2018 & 2019 - judge

Inspiring Young Women in STEM conference 2018 – volunteer

Science Rendezvous 2018 – volunteer